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REVIEW OF OCEANOGRAPHIC FEATURES RELATING TO NEONATE SEA TURTLE DISTRIBUTION AND DISPERSAL IN THE PELAGIC ENVIRONMENT: KEMP'S RIDLEY (LEPIDOCHELYS KEMPI) IN THE GULF OF MEXICO

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ABSTRACT

Young pelagic Kemp's ridley turtles may opportunistically utilize sargassum concentrations as refugia, and sargassum associates as sources of food. Association with sargassum or other floating objects involves risks as well as benefits. Potential food sources in the pleustal zone are abundant both within and away from surface convergences and sargassum rafts.

Coastal, shelf, and offshore currents vary during the hatchling emergence period. Hatchlings from a given annual cohort are exposed to different oceanographic, and disperal conditions, a form of bet-hedging that exposes the young to different levels of dispersal risk. Most hatchlings may reach, and become embedded in a boundary current off the natal beach regardless of current or wind conditions. Depending upon the type, location, strength, and paths of surface currents, pelagic stage Kemp's ridleys may either complete the developmental phase of the life cycle in the western Gulf of Mexico, or be transported to the east, entrained in the Loop Current, exit the Gulf of Mexico through the Straits of Florida, and drift to the north on the western edge of the Florida Current/Gulf Stream. Mean circulation patterns in the Gulf of Mexico based primarily on Lagrangian drifter data are discussed in support of dispersal pattern speculations.

Footnote 1, p. 5.
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The heterogeneity of the "wild" nesting/natal beach appears to be only superficially similar to Padre Island beaches, and differences between the two areas should perhaps be taken into consideration when evaluating the success of tag and release experiments performed in the latter location.

Footnote 2, p. 45.
*

Note: The swim frenzy, orientation and orientation cues, swimming speed and duration, and doubtful probability of hatchling loggerhead sea turtles reaching the Florida Current from the east coast of Florida (assuming a shelf width of ca. 30 km) during the "frenzy" period, is discussed by M. Salmon and J. Wyneken, 1987. The authors pointed out that the hatchlings eventually reach the western boundary of the Florida Current by post-frenzy-oriented movement. Results of this study were received after the present ms. was written.

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INTRODUCTION

Much of what is known about *Lepidochelys kempi* is summarized in Marquez (1986). Review of his and other summary accounts (Hildebrand,1963; Pritchard, 1979; Chavez, 1968; Carr, 1986 a, b; Meylan, 1986) and the works cited in them, clearly indicate areas of research that require increased investigative attention. Major aspects of *L. kempi* biology that are imperfectly understood include assessments of present population size, age and sex distributions, rates and causes of age-specific mortality, genetic variability, and the effectiveness of historical and present conservation efforts. It can be argued that the most conspicuous gap in knowledge of Kemp's ridley biology, however, is what happens to the turtles during the interval of time between first contact of hatchlings with the sea off the beaches of Tamaulipas, and their appearance as preadult benthic carnivores in shallow coastal waters of the eastern seaboard and the Gulf of Mexico.

The paper is presented in two parts. First, possible sources of food and refugia available to the young turtles in the open ocean are discussed. Second, the surface circulation of the Gulf of Mexico is discussed with respect to several possible current patterns that may explain, in part, why turtles of various sizes/ages have been observed in coastal waters at the times and geographic locations reported in the literature.

PART ONE
THE PELAGIC HABITAT

INTRODUCTION

Young *L. kempi*, (and other sea turtles) have an extended pelagic, more or less planktonic developmental stage in their life histories (Carr, 1986; Marquez, 1986). The widely held view that predator avoidance is accomplished by seeking refuge, perhaps actively, in floating aggregations of sargassum (e.g., Frick, 1976; Pritchard, 1979, 1980; Carr, 1980; Fletemeyer, 1978; Carr and Meylan, 1980; Pritchard and Marquez, 1973; Bennett and Kleerkoper, 1978; Witham, 1976; Hoffman and Fritts, 1982; Caldwell, 1969; Carr, 1986), and that species associated with sargassum (Fine, 1970) and/or surface convergence zones offer an abundant food source (Witham, 1980; Carr and Meylan, 1980; Carr, 1986; Marquez, 1986), is compelling, in that it offers a simple, logical explanation for how small turtles might make a living in the open sea. There are no ecological "strategies" (Hendrickson, 1980) without hazards, however, and the benefit-to-cost ratio of protection and food vs. predation, and dependence upon the vagaries of current and convergence locations, may be only marginally in favor of survival of the young turtles. A relatively recent major, and probably worsening hazard to survival of small pelagic turtles,

is hydrocarbon pollution and plastic debris that accumulate in surface convergence zones (e.g., Olson and Backus, 1985). Close examination of surface circulation patterns in the pelagic habitat may lead to a better understanding of the pelagic developmental phase of Kemp's ridley sea turtle.

Background

Although numbers fluctuate annually, currently 200-1500 adult female Kemp's ridley sea turtles nest each year (Klima, 1986; Marquez, Villanueva and Burchfield, 1986; Marquez, 1983; Caillouet, 1984; Fontaine et al., 1985). Byles' (1986) annual estimate of nesting females was 572, and reported that the number of nesting females has been decreasing by three percent per year since 1978. Nesting occurs along a 17 km stretch of beach in Tamaulipas State, Mexico, near the town of Rancho Nuevo, and just south of the Tropic of Cancer, 23 10' to 23 18'N., 97 45' W. (Marquez, 1976). Marquez (1986) summarized what is known about the areal, biological, environmental, and physiographic characteristics of the nesting beaches. Marquez (1986) and Hildebrand (1963) classified the nesting beaches as "high energy", with a shallow, flat nearshore bottom profile and several longshore sand bars and reef barriers. Generally such beaches are somewhat protected from the full force of ocean waves, and are more typically classified as "moderate-to-low energy", even though wave shock may be extreme on the seaward side of reefs and bars. Hopkins and Richardson (1984) reported

that the nesting beaches used by Kemp's ridley were stable, and subject only to slight erosion. A mixed saltmarsh/mangrove flora (e.g., Spartina and Rhizophora) (Hildebrand, 1963), and variation in beach composition and construction, from fine sand in some areas, to shell rubble and stones in other locations; from low (1-4 m) to rather massive (10-12 m) sand dunes along the nesting beaches (Chavez, et al., 1967), is evidence that "the" nesting/natal beach of Kemp's ridley is heterogenous along its 17 km length.

Marquez (1986) noted that data on currents were unavailable, but it appeared from his description of the nesting beach that there may be some local onshore focus of currents off Rancho Nuevo during the entire period of time from nesting of the adult females through hatchling emergence. He noted that drifting debris accumulates on the beach front as a result of these currents. Coastal currents are always alongshore, and do not "converge" on beaches except in catastrophic conditions such as hurricanes (M. Brown, pers. comm.). Surface drift may carry floating objects toward shore. These objects might accumulate on certain beaches due to wave refraction and bottom topography (e.g., headlands, reefs, shoals). It may be that Marquez (1986) spoke of waves rather than current convergences in his description of the beach. Variability of currents along the natal beach during hatchling emergence, discussed below, may play a role in the survivorship of neonate turtles. The presence of beach debris might not be evidence that hatchling or older turtles are steered toward the beach by currents.

Nesting occurs primarily between April and July, with highest frequencies in May and June. The last of the nesting females leave the beach by mid-July (Marquez, 1976; Chavez, Contreras, and Hernandez, 1968; Hildebrand, 1963). Within season and within year nesting frequencies are apparently variable.

Many workers have investigated the ocean-finding behavior of hatchling sea turtles. Though factors other than light cues have been suggested or implicated in experimental situations (e.g., Wibbels, 1984), hatchlings usually orient to light until they reach the ocean (Witham, 1980), and assume a pelagic lifestyle. Witham (1980) suggested that hatchlings exhibit a wave-orientation response; if there are waves they will swim into and through them. In the absence of waves, the animals may not swim purposfully in an offshore direction. Wibbels (1984) and McVey and Wibbels (1984) reported similar behavior in 18-24 month old captive-reared turtles released under experimental conditions. Stonebrunner et al. (1982) summarized hypotheses and observations of hatchlings swimming out to sea, (`in search of sargassum'). It seems clear that most Kemp's ridley hatchlings swim more-or-less directly out to sea immediately upon reaching it. One would expect exceptions to this general tendency both between individual turtles, and under particular environmental conditions. Convincing direct evidence in support of a usual seaward swimming response by Kemp's ridley hatchlings has been

documented (Hildebrand, 1963; Carr, 1980; Hendrickson, 1980; Witham, 1980; Pritchard, 1969).

Survivorship rates of pelagic Kemp's ridleys are unknown. Marquez et al. (1981), speculated that theoretical survival rates to year seven (the approximate age of sexual maturity) is 0.025. Pritchard (1980) estimated that, based upon tag returns, survival to sexual maturity was 2-3 per 1000 eggs. According to Pettingel (1979), perhaps one out of 100 turtles from Rancho Nuevo survives to the adult stage. Egg, hatchling, and post-hatchling pelagic stage mortality is undoubtedly high, as with younger stages of all species, although nest/egg protection efforts at Ranch Nuevo have reduced loss of the first two stages somewhat. Headstarting efforts may or may not have mitigated the loss of pelagic stage individuals, although the success of all conservation efforts thus far attempted is unproven (see Mrosovsky, 1983; Hildebrand, 1982; Marquez and Perez, 1982; Crouse, 1985; Marquez, 1986, for reviews).

Marquez (1986) summarized the survival value to hatchlings of swimming away from the beach. The chief immediate result of such behavior involves getting the vulnerable hatchlings to the beach, through the surf and waves, over shoals, sandbars and reefs, and away from numerous predators found in these areas, in the shortest time possible. Pritchard and Marquez (1973) pointed out that hatchlings must swim actively for some hours or days to avoid being thrown back up on the beach from which they came. Carr and Meylan (1982), among others, have reported strandings of post-hatchling turtles after storms or hurricanes.

In discussing his "lost year" work, Carr (1986b) suggested that hatchlings thrown back upon their nesting beaches must have been trapped in local eddies. He also discussed the strong open-sea orientation of hatchling sea turtles, and explained that the "swim frenzy" observed by numerous workers was clearly developed to take them into longshore currents, although he felt that, "It may be a straw in the wind that there is a seasonally strong onshore movement of currents along the Texas coast during hatching time" (Carr, 1980). Again, it is important to distinguish between the drift of surface water resulting from onshore winds, and onshore currents; Carr referred to the wind driven flow of shelf water off the Texas coast (see Shaw et al., 1985). Should there be a tendency for the turtles to swim either against or with alongshore currents after leaving their natal beaches, they would be at some risk of being re-deposited on the beach.

Cochrane and Kelly (1986) found that the only shore-normal current flow induced by the winds is in an offshore direction (a return flow) at the point where winds are exactly normal to the shore. The effective difference between surface drift and "onshore" currents to the net movement of hatchling turtles may not be significant, but it precludes the construction of a paradigm that I originally wished to develop relating both the formation of arribadas and initial hatchling orientation off the

natal beach to onshore current convergences. Regional (rather than onshore convergent) currents probably influence the dispersion of hatchlings, although cause and effect relationships are entirely speculative. When present, strong longshore currents off the natal beaches during the hatching period probably play an important role in determining when and where neonates cross the continental shelf, as it is presumed they do, to arrive in the open sea.

In the sense discussed below, variation in the chronology of events early in the life cycle of a given year class of Kemp's ridley may be viewed as a form of "bet-hedging" in the species. Females may nest more than once per season, and second and subsequent nests may be a mile or more away from the first. Within-season internesting frequencies are variable, and may depend upon physiological responses to appropriate environmental cues such as surf conditions and possibly storms (Hildebrand, 1963). Not all of the hatchlings from a single nest may leave it at the same time, and at least some between-arribada nesting occurs (discussed by Marquez, Villanueva, and Burchfield, 1986). Nesting occurs during a four month period (April-July), and hatchlings thus leave the beach over a four month period (June-November). Although most nesting occurs during the May-June period as documented earlier, a given year-class of Kemp's ridley hatchlings are able to test a range of beach and offshore conditions.

It is incorrect to assume that all young turtles produced during a single nesting season, or even a single arribada are exposed to equivalent hazards when they enter the waters of their natal beaches and assume a pelagic existence. An exception to this might occur in the event of beach contamination by an oil spill (Lutz, Lutcavage and Bossart, 1986; Vargo and Lutz, 1986).

THE PELAGIC HABITAT OF YOUNG KEMP'S RIDLEY IN THE GULF OF MEXICO

Sargassum

Floating (Galt, 1985) and depth-keeping species (Olson and Backus, 1983), and floating objects such as tar balls, plastics, and the like (Kennedy, 1972; Frazier, 1980) are concentrated for varying periods of time in surface convergence zones (e.g., Gooding and Magnuson, 1967; Ewing, 1950; Weiss, 1968; Falber and Woodcock, 1952; Deacon, 1942; Wong, et al., 1974). Windrows and

dense patches of sargassum have been mentioned by numerous observers from at least the time of Columbus' voyages in the 1400's (summarized by Deacon, 1942), and concentrating phenomena such as Langmuir cells and ocean fronts have been generally known for many years. In the western North Atlantic, masses of sargassum are concentrated in the Sargasso Sea (Winge, 1923; Woodcock, 1944; Teal and Teal, 1973; Butler et al., 1983). Pelagic sargassum, or Gulf Weed (primarily Sargassum natans and S. fluitans) is also commonly seen in the Gulf of Mexico, but it is not as often found in concentrated rafts or driftlines approaching the size of those found in the vicinity of the Sargasso Sea.

Parr (1939) noted that there were conspicuous differences in the health and abundance of sargassum between the Gulf of Mexico and the Sargasso Sea, and reported that, "...weed in the Gulf of Mexico is in an unhealthy state in contrast with the Sargasso Sea". Bortone, Hastings and Collard (1977) described the depauperate fish fauna associated with sargassum in the Gulf of Mexico compared to the Sargasso Sea, and Collard (1979) reported that neustonic zooplankton in the eastern Gulf of Mexico was impoverished compared to the western North Atlantic. Fleminger (pers. comm.), felt that a number of copepod species were for some reason not found in the plankton of the Gulf of Mexico a short time after entering it from the Caribbean Sea through the Yucatan Straits. His general observation is confirmed, in part, by Turner et al. (1979) and Turner and Collard (1980). While convincing quantitative studies have not been published, it seems that substantive qualitative differences may exist between the surface-associated fauna and flora of the Gulf of Mexico and the Sargasso Sea region of the western North Atlantic.

On occasion, dense mats of sargassum have been observed in the Gulf (Ogren, pers. com.; Captain R.E. Millender, pers. comm.), although such accumulations are not common, in my experience. During more than 60 cruises in the eastern Gulf of Mexico during which attention was given to recording the occurrence of sargassum, it was always seen; usually in widely separated, small clumps, regardless of position or time of year. Seldom were extensive windrows or aggregations of the weed seen, except on those (relatively few) occasions when the sea had been calm for an extended period of time, or when near the Loop Current.

After observing a period of frenzied swimming behavior in captive green turtle hatchlings, Frick (1976) concluded that they probably travel steadily for 24 hours after leaving the beach. She observed the course of released hatchling green sea turtles to be into the current (surf?) and normal to the shore. The turtles swam independently and, once they had established a course, kept to it in spite of natural and introduced obstacles. She further suggested that hatchling green sea turtles swim offshore to longshore currents to find sargassum. Kremer and Bennett (1981) reported that the quantity of yolk available as an energy source to hatchling loggerheads was not sufficient to

sustain them during travel from the south Georgia coast to a major oceanic current such as the Florida Current or Gulf Stream, but supported the idea that frenzied swimming activity during the first few days after emergence would enable them to travel some distance offshore. Caldwell (1962) reported, however, that one captive sea turtle that would not eat swam actively for five months before it starved to death, indicating that yolk energy reserves may not absolutely limit the swimming range of a neonate turtle. Frick (1976) observed a neonate green turtle dive and consume a ctenophore prior to encountering sargassum in which it subsequently rested.

Fletemeyer (1978) summarized historical records of hatchling sea turtles associated with sargassum, and observed loggerhead hatchlings rest and shelter in sargassum when it was present close to shore. Owens (1983) reiterated that the most commonly accepted hypothesis concerning neonatal distribution suggests an association with drift lines which contain sargassum or flotsam. Witham (1974) observed two live hatchlings on top of a floating board underneath which several Coryphaena were feeding. Capture of these fish revealed that one of them had eaten eight posthatchling loggerheads and one green turtle about two weeks old. Pritchard and Marquez (1973) suggested that Kemp's ridley post-hatchlings drift passively with sargassum. This association was also thought to be the case with green turtles (Bennett and Kleerkoper, 1978; Carr and Meylan, 1980), and loggerheads (Carr 1986; Smith 1968; Caldwell, 1969). Many other authors have either suggested or observed that small sea turtles are associated with pelagic sargassum (Weiss, 1968; Fine, 1970; Ryland, 1974; Caldwell, 1969; Witham, 1976; Hoffman and Fritts, 1982).

The geographic and temporal distribution of pelagic sargassum in the western North Atlantic is primarily determined by surface winds and current patterns (Butler et al., 1983). Carr (1980) was aware of this when he stated, "An understanding of shear-line geography is critical to the search for the "lost" post-hatchling stage of sea turtle ecology.... Until this information is available our knowledge of the life cycle is seriously incomplete, and effective conservation is handicapped. To achieve better knowledge of shear-line distributions and seasonality seems essential to an understanding of sea turtle ecology". Carr et al. (1982) reiterated the importance of understanding shear lines, and later stated unequivocally (Carr, 1986) that the biology of young sea turtles could not be understood by biologists in the absence of a clear understanding of surface convergence areas (which explain aggregations of sargassum and its associates, such as post-hatchling sea turtles). Carr (1986), also stated that, "It now seems well established that hatchling sea turtles go into sargassum driftlines, if there are any within their initial locomotor range. (The) accumulated reports clearly indicate that hatchlings not only go into sargassum rafts, but remain in them for long periods of time. (The) sargassum refuge theory is now proven fact.... (Convergences and downwelling) action is fundamental to the

ecologic organization of the epipelagic, and I have elsewhere suggested (Carr, 1986b) that there would be no sea turtles, of the kinds we know, if there were no fronts".

Given that hatchling Kemp's ridleys energetically swim out to sea after leaving their natal beaches and take refuge in sargassum rafts when they encounter them, how they make a living there is less certain. Hypotheses concerning sargassum as a refuge for small sea turtles should note that the distribution and abundance of sargassum in the Gulf of Mexico is more diffuse, and less predictable in its temporal and areal distribution than it is in the Sargasso Sea or the western edge of the Gulf Stream system, which has generally been used as a model. A majority of reports of small sea turtles associated with sargassum have come from the east coast of the U.S., and there are relatively few records from the Gulf of Mexico. There are no published reports of Kemp's ridleys associated with sargassum.

Substrate type is thought to be the most important environmental factor in determining the organization and composition of benthic marine communities (Collard and D'Asaro, 1973). Pelagic sargassum is often referred to as a floating benthic (or pseudobenthic) habitat (Butler et al., 1983), and it provides a substrate for a unique assemblage of sessile plants and animals, many of which are not found elsewhere (Fine, 1970; Morris and Mogleberg, 1973; Butler et al., 1983). A number of other species, such as Planes minuta, Portunus sayi, and Histrio may, to extend the benthic analogy, be considered demersal, in that they are associated with the sargassum substrate, but may leave it to forage. Juvenile fishes of many species, notably the filefishes, Seriola, Coryphaena, butterfishes, exocoetids, and others, are temporary associates of sargassum (e.g., Bortone, Hastings, and Collard, 1977). The young of many species of fishes seek shelter under any sort of floating material in the open ocean (e.g., Mansuetti, 1963; Zann, 1980) including sargassum, rafts, logs, jellyfishes, and large sea turtles (Gooding and Magnuson, 1967). Adult fishes, such as tunas, sharks, amberjacks, and billfishes, are also found near and underneath sargassum. Many of the larger fishes are predators which, it is thought, are attracted to the weed by the smaller (potential) prey species sheltering there. Gooding and Magnuson (1967), however, made an important observation: Only one of the many large predators, Seriola rivoliana, was seen to capture one of the sheltering "prey" individuals. Larger fishes characteristically soon leave the vicinity of sargassum and other rafts.

Gooding and Magnuson (1967) suggested a number of plausible reasons for the accumulation of fishes around sargassum and other floating objects: Protection from predators; concentrations of potential prey species; cleaning stations, and (citing Suyahiro, 1952), shade to protect them from thermal stress.

There is no information on whether Kemp's ridley hatchlings climb onto sargassum as some other species, particularly loggerheads, have been observed to do (Carr, 1986). Information is also lacking on whether young sea turtles, in general, may take refuge in clumps of sargassum and climb onto its surface in order to avoid perceived predators such as fishes, which are known to prey on small sea turtles (Witham, 1974), or whether such

behavior is a stereotypic response to floating objects in general, whether to avoid predators or for some other reason(s). The carapace of Kemp's ridley post-hatchlings can not be said to be cryptically colored, at least to any significant extent, and should be visible to aerial predators while resting on the surface of sargassum. Frick (1976) observed that frigate birds caused the green turtles she was following in the water to dive, whereas swimmers did not cause them to take evasive measures. Thus, some presumptive evidence exists that very young turtles, perhaps at the end of the swim-frenzy period, purposefully use sargassum as a refuge. To my knowledge, no permanent member of the sargassum community (Butler et al., 1983) is capable of eating small sea turtles.

Many observations of small sea turtles (Carr, 1986) might justifiably lead one to conclude that there is significant survival value in a sargassum association. Hildebrand (1980) and others have found stranded neonate sea turtles covered with encrusting organisms such as bryozoans that also grow on sargassum, thus providing indirect evidence that the turtles had spent an extended period of time in the weed. The presence of encrusting organisms on small sea turtles may also be attributed to the random attachment of the planktonic larvae of bryozoans and the like to any floating object, however. Except for aggregations of sargassum associated with fronts, rafts of any size in the Gulf of Mexico may be relatively short-lived. Rafts, mats, and wrack lines of sargassum constantly break up and re-form in different configurations and in different locations due to waves and storms, or they sink due to the weight of encrusting organisms or wind stress. When considering the survival value of sargassum to young sea turtles, it must be determined how long (on an average basis, at least) sufficient quantities of coherent masses of sargassum are available for the turtles to take refuge in. From personal observations in the Gulf of Mexico, I suspect that rafts of the weed sufficiently large to afford protection to a small sea turtle are present infrequently, even, as seems to be the case, when both the turtles and sargassum are often found to be concentrated in the same area, by the same mechanisms (i.e., certain types of surface convergences).

Based upon the scanty available evidence, I suggest that Kemp's ridley post-hatchlings opportunistically use sargassum patches as refugia. While their oceanic survival rate is enhanced to some degree by the presence of sargassum, their success as members of the surface plankton does not altogether depend upon its

presence. Carr (1986), suggested that it is not sargassum *per se* that is of crucial importance to post-hatchling sea turtles, but the accessibility of a front along which downwelling and concentrations of food occur.

Sources of Food

Organisms found often or only in association with pelagic sargassum in the western North Atlantic have been described by Fine (1970), Morris and Mogleberg (1973) and Butler et al. (1983). Carr and Meylan (1980) examined the stomach contents of 15 green turtle hatchlings that had been washed ashore as a result of Hurricane David in 1979, and found that the most prevalent food items were bits of sargassum in the five animals that had food in their stomachs. They also recovered the sargassum snail, *Litiopa melanostoma*, and the pelagic snail, *Diacria trispinosa* in one turtle each. I have been unable to find information on the forage of pelagic Kemp's ridley. Nierop and Hartog (1984) reported that loggerheads were known to eat epipelagic animals including the isopod, *Idotea metallica*, which is often associated with tar balls. In captive situations, hatchling Kemp's ridleys remained healthy and grew normally on a wide variety of foods, including lettuce, chopped fish, shrimp and a pellitized food similar to "trout chow" (Marquez, 1986; Fontaine et al., 1985).It seems likely that young pelagic Kemp's ridleys could rather easily find suitable forage when in sargassum mats, as a rather broad diversity of animals and epiphytes are always found to be associated with the weed. It is unknown whether Kemp's ridley manufactures cellulase, or harbors symbiotic bacteria or protists that produce it. There are no published data on sargassum as a food source for the species. Bits of sargassum in the stomachs of young green turtles as reported by Carr and Meylan (1980) might be accounted for by the animals' deriving nutritional benefit from small animals attached to the sargassum, rather than from the weed itself. Post-hatchling Kemp's ridleys may swim from patch to patch of sargassum when it is no longer efficient for them to feed on a given raft, or when the weed is dispersed due to wave action. In such cases a turtle might swim downstream, and overtake sargassum drifting with currents, or swim across the direction of current flow until it encountered a food source, as suggested by Ogren (pers. comm.). A similar possibility was suggested by Witham (1980).

While De Sola and Abrams (1933) determined that the length of juvenile Kemp's ridleys gut seems to be characteristic of herbivores, it is not known whether gut morphology changes with age in the species. Limited observations of the young of other species of sea turtles, and the feeding behavior of captive Kemp's ridleys suggest that Kemp's ridley has a broad diet width, and is a nutritional generalist during its young pelagic stage. An apparent change in forage preference occurs once the turtle assumes an inshore demersal/benthic existence, and the diet is primarily composed of portunid crabs (Dobie et al., 1961).

Several other types of benthic food items have been recorded, including other crustaceans, gastropods, bivalves, echinoderms, jellyfish and squids (summarized by Marquez, 1986). The diet of benthic-stage Kemp's ridley may change not only because of a developmental habitat shift but because of the greater availability of crustaceans, and increased efficiency in search

and handling times. The species clearly eats crabs and, on occasion, certain pelecypods and a variety of other benthic invertebrates. It is not clear whether the ingestion of such prey items as starfishes is accidental, or a broadening of diet width when preferred forage species are rare.

Surface convergences are the result of different ocean processes, and differ in terms of the frequency of their occurrence, longevity, and scale. Because of these major differences, attempts to relate the possible abundance of food available to surface-associated animals, such as small pelagic sea turtles, should be made cautiously, and only with respect to specific kinds of convergences. For example, ocean fronts and Langmuir cells are significantly different in terms of the oceanographic conditions under which they occur, and in the extent and persistence of the organization of surface objects associated with them. Langmuir circulation occurs only in near-calm seas, and cell convergences are parallel to each other, spaced but a few meters apart. "When they are present, little turtles are never more than a few breast strokes away from one" (M. Brown, pers. comm.). Convergence zones along ocean front boundaries extend for large distances, but when they are present in a given region, may be hours or days away from a drifting or slowly swimming small turtle. Except for their general locations and statistically predictable frequency of occurrence, convergences are not permanent features of the open-ocean landscape. A general discussion of ocean convergences and the factors that cause their formation was presented by Galt (1985). I suggest that there may be a more parsimonious way to explain how turtles find enough food to sustain them in the open sea when they find themselves, as they must for varying periods of time, away from convergence-related food concentrations.

Biologists investigating zooplankton <u>in situ</u>, have shown that the near-surface waters of the oceans are often inhabited by, among others, a wide diversity and abundance of gelatinous animals such as colonial radiolarians, salps, ctenophores, siphonophores, jellyfish, pteropods, larvaceans and heteropods (e.g., Hamner, et al., 1975; Swanberg and Harbison, 1980; Madin, Cetta, and McAlister, 1981; Harbison, Madin, and Swanberg, 1978). "Marine snow" is also abundant in near-surface waters of the open ocean (Silver, Shanks and Trant, 1978). Marine snow consists of often macroscopic aggregations of mucus from the cast-off "houses" of larvaceans, filtering nets of pteropods, and residues of scyphozoans and other gelatinous zooplankters. These aggregations appear to be organically rich, and have embedded in them fecal pellets, flagellates, bacteria, diatoms, and both dead and living

crustaceans. Marine snow is easily visible to divers in the water, and presumably would be to turtles as well. They are a potential source of food which deserve additional investigative attention. Many of these animals are rarely or never caught in plankton or neuston nets because of their fragility. A small Kemp's ridley physiologically capable of eating these animals, many of which manufacture mucous food webs upon which they entrap other animals, would likely find no lack of food anywhere in the ocean. All that the turtles would be required to do to capture the gelatinous zooplankton is possess the ability to see them (see Mayer, 1910, cited by Witham, 1980, for observations of gelatinous zooplankton on the ocean surface), and be able to dive a few meters to catch them. Evidence is adequate to assume that young turtles use primarily visual cues to locate food (Fontaine et al., 1985; Manton, Carr, and Ehrenfield, 1968); and they are able to dive even as hatchlings (Frick, 1976). The leatherback sea turtle is well-known to feed on jellyfishes (Lutcavage and Lutz (1986), and green and loggerhead sea turtles have been observed to feed on jellyfish and ctenophores (Salvini-Plawen, 1972; Frick, 1976). Pelagic Kemp's ridleys may also feed on gelatinous zooplankters.

Because of the potential availability of food in the form of sargassum-associates, and near-surface gelatinous zooplankton, I agree with Carr (1986b) that lack of an adequate food supply is not a major cause of mortality in young L. kempi.

Survival In The Pelagic Environment

Small drifting sea turtles must successfully avoid predation, find food, and stay in water whose quality and temperature ranges are within the turtle's physiological tolerance limits. An unknown number of post-hatchlings may be transported by currents to areas from which they cannot return to reproduce. Many post-hatchling sea turtles probably fail to meet these challenges but

we know nothing about survival rates for this period in their life. Shelter and food sources have been briefly discussed, and dispersal by currents is discussed in Part 2. "Water quality" -- in the broadest sense of the term, including oil pollution and sheet plastics--has been summarized by Balazs (1985) and Marquez (1986). The distribution of oil and plastics in the sea has been discussed by Horn and Backus (1970); Wong, Green, and Cretney (1974), and Frazier (1980). It seems reasonably certain that post-hatchling sea turtles are increasingly at risk from pelagic pollutants.

Except for the observed tendency of young sea turtles to enter sargassum rafts when they they can see or otherwise sense them, and with the caveat that no sargassum or other floating debris may be in their immediate area, the only evidence that I am aware of that post-hatchlings actively attempt to avoid predators is that of Frick (1976), who reported that the turtles responded to the presence of frigate birds by diving. The relatively small

size of months-old pelagic Kemp's ridley (summarized in Marquez, 1986), and the abundance of large predatory fishes (dolphins, tunas, sharks, etc.) in and near convergence zones and/or sargassum rafts; the absence of known predator-avoidance behaviors (excluding aggressive behavior in captive situations), and the absence of information that might indicate that Kemp's ridley is unpalatable, or poisonous to eat, I must tentatively conclude that the probable wide dispersion of the smaller animals in the open ocean is their chief means of avoiding predation.

SUMMARY AND CONCLUSIONS

Although Kemp's ridley nesting occurs in the form of arribadas, not all hatchlings within a given year-class leave the nest at the same time, or from the same location on the beach. Longshore currents off the nesting beaches change in strength, and possibly direction during the period of time that hatchlings begin their swim offshore. Thus, individual groups of neonates face different environmental conditions and hazards as they approach and enter the sea, which is suggested to be in a non-evolutionary sense, a form of "bet-hedging" in the species.

Hatchlings energetically and purposfully swim out to sea principally to avoid predation and to avoid being redeposited on the beach by waves. The duration of the swim frenzy and possible exercise of "choice" by the turtles to terminate the swim, are unknown. When hatchlings encounter currents offshore they are entrained in, and transported by them.

Should hatchlings encounter sargassum either near or offshore they may opportunistically enter it to rest, seek refuge, or to feed on sargassum associates. The turtles' behavior with regard to sargassum, however, may be a stereotypic response to any floating object of sufficient size to be perceived by them. Sargassum and sargassum-associates in the Gulf of Mexico may be substantially different than in the western North Atlantic, especially in and near the Gulf Stream system. In comparison, Gulf of Mexico sargassum is commonly widely dispersed, less in total quantity, depauperate in terms of its animal associates, and its occurrence less predictable in space and time. Most observations of post-hatchling turtles associated with sargassum have been in the North Atlantic proper. Sargassum may not play as important a role in the ecology of young sea turtles in the Gulf of Mexico as it does off the east coast of the United States.

Given that plankton, including sargassum, are concentrated by winds and surface convergences of various types, it is unlikely that post-hatchling sea turtles and sargassum would not be found, on occassion, at the same place and time. The young turtles would increase somewhat the frequency of encountering sargassum by increased swimming activity.

Sargassum rafts and convergence zones as discussed by Carr (1986b) may provide post-hatchlings with a concentrated source of food, but nutritional requirements of the young turtles can probably be met anywhere in the pleustal zone in the form of marine snow and gelatinous zooplankton. *L. kempi* may be a dietary generalist throughout its life.

The importance of sargassum to small pelagic stages of Kemp's ridley in the Gulf of Mexico remains unknown. While the crucial role of surface currents in the distribution of post-hatchlings seems certain, surface convergences may *per se*, present more hazards than benefits to the turtles in way of attracting predators historically, and pollutants more recently.

PART TWO

GULF OF MEXICO CIRCULATION AND DISPERSION SCENARIOS FOR THE PELAGIC STAGE OF KEMP'S RIDLEY

INTRODUCTION

There is general agreement that hatchling sea turtles more-or-less passively drift with surface currents for a year or more upon conclusion of an initial energetic swim (the "swim frenzy") offshore from their natal beaches (e.g., Frick, 1976; Witham, 1976; Pritchard, 1979; Carr, 1980; McVey and Wibbels, 1984; Carr, 1986; Meylan, 1986). Hatchling and headstarted Kemp's ridleys generally swim on a steady course directly out to sea from the beach, although they are known to make compensatory course changes to resist longshore movement by waves and currents (Wibbels, 1984). They circumvent physical objects in their paths, such as swimmers, but may rest or take refuge in patches of sargassum (Fletemeyer, 1978; Frick, 1976), and it has been suggested that the turtles swim out to sea in order to find sargassum (Frick, 1976; summarized in Stonebrunner et al., 1982). It is not known whether the young turtles stay with sargassum when they encounter it close to the beach, or whether they are "programmed" to continue to swim for a fixed time interval, or until their energy supply (residual yolk) is depleted (Frick, 1976; Kremer and Bennett, 1981). Whether initial swimming involves innate exploratory behavior or some choice is exercised in where or when they terminate the swim frenzy period is unknown. Considerable presumptive evidence indicates that the major initial objective of the newly hatched turtles is to distance themselves from the beach (summarized in Marquez, 1986). Hatchling turtles likely slow or stop directional, purposeful swimming at some time after the swim frenzy period, and it is assumed that they then become relatively passive drifters whose subsequent net movement is determined by surface currents (Witham, 1980; Carr, 1980; Carr, 1986) such as the Mexican (Sturges and Blaha, 1976) and Loop Currents in the Gulf of Mexico (Brown, 1986), and the Gulf Stream system in the North Atlantic (Pritchard and Marquez, 1973), and by local eddies shed by these currents. The potentially important affects of wind on the movement of drifting turtles have not been considered.

Evidence for a planktonic developmental period in the life history of Kemp's ridley and other species of sea turtles is convincing. Except for strandings usually attributable to onshore storm winds and waves (Carr, 1986; Caldwell, 1969; Carr and Meylan, 1980), or thermal shock in post-pelagic juveniles and subadults (Schwartz, 1978; Ogren and McVey, 1981; Fontaine et al., 1985), post-hatchling individuals are not captured or observed in nearshore waters. Neonate and post-hatchling sea turtles are probably not capable of sustained swimming speeds much above one km/hr (Frick, 1978; Witham, 1976), a speed slower than would be required for them to have reached distant recovery areas reported by numerous workers. The duration and speed of swimming in supposedly "passively"

drifting small turtles is, however, unknown. Distribution records are summarized in Ogren, 1985, and Marquez, 1986). The drifting period may last a year or more, or until such time as juveniles reappear in coastal waters throughout the Gulf of Mexico and along the eastern seaboard of the United States.

During the pelagic drifting period, small turtles are thought to accumulate in areas of surface convergences some of which, dissipate then re-form, as Langmuir cells do (Carr, 1986). Both turtles and their food sources, thought possibly to be sargassum-associates, accumulate in this way (see Part 1), and the turtles are protected from overwhelming predation by sheltering in the weed. Carr (1986) summarized direct evidence of young loggerhead and green turtles associated with sargassum in or near major currents such as the Gulf Stream.

General schemes have been proposed to explain the probable current-mediated transport of young Kemp's ridleys from their natal beaches near Rancho Nuevo on the west coast of Mexico, to where they reappear as preadults in coastal waters (summarized in Marquez, 1986; Carr, 1986). It is not known with certainty whether Kemp's ridley subadults observed all along the eastern seaboard (Marquez, 1986; Henwood and Ogren, 1987) make their way back into the Gulf of Mexico, or some of them do, or how they may accomplish this. It has been suggested that Kemp's ridley individuals that have been swept out of the Gulf of Mexico are lost from the breeding population and become waifs (Hendrickson, 1980), while others have suggested that remigration into the Gulf of Mexico is likely (e.g., Pritchard, 1969; Pritchard and Marquez, 1973; Byles, 1985; Henwood and Ogren, 1987; Lazell, 1980; Meylan, 1986). Carr (1980) considered both possibilities. How individuals of breeding age/size locate the nesting beaches off Rancho Nuevo remains

unknown (Owens, Crowell-Comuzzie and Grassman, 1985; Koch, Carr, and Ehrenfeld, 1969, discussed other species), but mechanisms causing the adults to congregate and together participate in arribadas have been proposed (Hendrickson, 1958; Mora and Robinson, 1982).

It has been apparent to turtle investigators that Kemp's ridley must either undergo part or all of the pelagic phase of its life cycle in the Gulf of Mexico (e.g., Hildebrand, 1980), or that some or all of a given year-class are swept out of the Gulf with the Loop Current, to complete the remainder of the pelagic phase in the North Atlantic (e.g., Pritchard and Marquez, 1973). As Carr (1980) said, "...understanding the early life history of sea turtles is the most important unsolved problem in sea turtle biology."

What follows is a speculative consideration of the surface circulation of the Gulf of Mexico based on recent work by physical oceanographers, and some possible distributional scenarios for the pelagic stage of post-hatchling Kemp's ridley. Enough may now be known about the end-point distributional patterns of Lepidochelys kempi juveniles, pre-adults and adults (summarized in Marquez,

1986; Henwood and Ogren, 1987), and the mean surface circulation patterns of the Gulf, to construct an hypothesis about where and how post-hatchling stages in the pleustal zone are transported by surface currents or the movement of eddies in which the turtles may be embedded.

General Circulation Patterns in the Gulf of Mexico

The Gulf of Mexico receives its major source of water through the Yucatan Straits from the Caribbean Sea. This stream of water forms the Gulf of Mexico Loop Current, whose meanders and eddies are components of the anticyclonic ocean basin circulation of the eastern Gulf. Anticyclonic eddies (or "rings"), shed periodically from the Loop Current migrate into and across the western Gulf of Mexico, which results in an overall clockwise circulation pattern in the northwestern Gulf. Sturges and Blaha (1976) suggested that a western boundary current similar to the Gulf Stream system dominated the Texas/Mexico continental shelf and slope. Although the short and longer term behavior and exact causes and periodicity of ring shedding by the Loop Current require additional study (Sturges and Evans, 1983; Waddell, 1986), there is general agreement among physical oceanographers that circulation in the eastern and western Gulf basins are coupled in a complex way, and that the direction of offshore currents in the western basin are primarily the result of Loop Current events. Three examples of suggested general surface circulation patterns are shown in Figures 1, 12, and 13.

Whereas the boundary current of the western Gulf of Mexico is believed to be driven principally by eddies of the Loop Current, shelf circulation patterns throughout the Gulf of Mexico are primarily wind driven (Sturges, 1986; Cochrane and Kelly, 1986). In shelf waters along the north-south trending coasts of northeastern Mexico and southern Texas, southeasterly winds tend to induce a general northerly flow. Along east-west coasts outer shelf currents flow to the east during most of the year (Shaw et al., 1985).

A non-technical overview of shelf-slope boundary surface current patterns based upon recent field and modeling investigations (summarized in Wallcraft, 1986; Waddell, 1986), is approximately as follows. Given coupling of boundary currents between the western and eastern basins (i.e., across the Mississippi Delta region), net slope boundary water transport is generally clockwise throughout the Gulf of Mexico (Bruchs, pers. comm.; Fig. 1) with the exception of cyclonic flow off the Texas coast. In the absence of coupling, eastern and western basins may have, for variable periods of time from several months to a year (Elliott, 1982), essentially independent clockwise circulation patterns.

Eastern Gulf of Mexico Loop Current

The western boundary of the Loop Current rarely extends west of 90 longitude, and its eastern boundary protrudes rarely onto the west Florida shelf, although interleaving filaments of warm Loop Current water may be advected across the shelf/slope boundary as a result of the meandering behavior of the Loop Current front (Sturges, 1986). Variation in the position of the northern boundary of the Loop Current have been discussed by Sturges and Evans (1983), and Thompson (1986).

Based upon 1965-1966 data, Liepper (1970) suggested that northern intrusions of the Loop Current had an annual cycle, beginning in the spring and reaching highest latitudes in the summer and fall. During its northernmost penetration the current was either continuous from Yucatan to the northeast Gulf, or a northern eddy detached from the current (to drift west in the fall) leaving a remnant of the Loop Current in the southeast Gulf (Figs. 2, 3, from Molinari et al., 1977). Maul (1975) reported a similar pattern from 1972-1973 data. Molinari et al. (1977) noted that the Loop Current sometimes follows an almost straight path from the Yucatan Straits to the Straits of Florida, and at other times it extends far to the north as an anticyclone. Their data, from the period 1974-1977, showed that the Loop Current extended farthest north during the winter months. Prior to 1974, winter intrusions north of 26 N (a parallel connecting Cape Romano and the U.S.-Mexican border) had not been reported. Actual and model circulation patterns in the eastern Gulf of Mexico have been summarized and discussed in Sturges and Shang (1978), Waddell (1986), and Wallcraft (1986).

Western Gulf of Mexico

Using a two-layered time-dependent hydrodynamic model with a free surface to investigate Loop Current stability, Hurlburt and Thompson (1980) concluded that anticyclonic eddies can be shed in a regular manner from the Loop Current with no time variation in inflow transport. Smehil, Behringer and Molinari (1978), reported that a three gyre circulation pattern was observed in the Gulf during October-November 1976: The Loop Current in the east, a detached eddy in the central Gulf, and a gyre in the western Gulf, which filled the deep basin. A similar pattern occured in 1967, 1969, and 1972, and it was suggested that a large exchange of water between the eastern and western Gulf occured at 90.5 W, particularly in the spring (Smehil, Behringer, and Molinari, 1979). Recent studies have shown that, on an annual basis, there are often from one to three closed, westward-drifting rings in or entering the western Gulf as a result of eddy-shedding or breakdown of the northern portion of the Loop Current (Lewis, 1984; Brooks, 1984; Kirwan et al., 1984; Waddell, 1984; Wallcraft, 1986).

Lewis (1984) reported the movements of a Lagrangian drifter buoy (No. 3374) seeded in a warm core ring of the Loop Current in October, 1982 and tracked until August, 1983 (Figs. 4, 5). He described its movement as follows:

> Drifter 3374 was deployed in a ring in October 1982 and showed a westward translation, an oscillatory period after coming in contact with the Mexican coast... and then a period after July 1983 during which the buoy left the ring and moved toward the east... The location at which the drifter left the ring coincides with a region
>
> where large eastward transports have been observed. This eastward flow is a result of a combination of the flow pattern of the north limb of the anticyclone and the south limb of a cyclone which is typically found directly north of the anticyclone. Numerical experiments show that a cyclone can be shed from an anticyclone as the latter feels the effects of a western boundary (Smith and O'Brien, 1983).

Eastward transports described by Lewis (1984) have also been documented by Cochrane and Kelly (1986), and by Shaw et al. (1985). Weisenberg (1983) described an east and south flowing jet along a front separating coastal water in the Mississippi River plume and the northern limb of a large (200 km in diameter) anticyclonic Loop Current eddy near 28 53' N, 88 31' W, in December, 1982. His direct observations of the front were confirmed by remote sensing imagery from the NOAA-7 radiometer (AVHRR) and the NIMBUS-7 coastal zone color scanner. This jet, located somewhat south and east of the Mississippi delta may have resulted in the transport of floating organisms and debris observed by Weisenberg, from the western to the eastern basin of the Gulf.

Drifter No. 3375 was seeded in a ring in July, 1983. It drifted south after a short period, then came under the influence of an earlier ring that had already migrated to the Mexican shelf boundary (Lewis, 1984).

Brooks and Laegickis (1982) estimated the spin-down time for rings was on the order of two-four months after their translation to the western Gulf slope. Lewis (1966) described the path of drifter buoy 1599 (Fig. 6), and Kirwan et al. (1984) described the path of drifter No. 1600 (Fig. 7), which were tracked from November, 1980 through May 1981. These buoys exhibited the same general pattern of movement as those described by Lewis (1984). Waddell (1984) reviewed the track of drifter buoy No. 3350, which was released in a Loop Current eddy in April, 1984, and followed until September, 1984 (Fig. 8). After making three complete revolutions in the eddy, buoy No. 3350 migrated southwest to the Mexican shelf-slope boundary. Waddell (1986), summarizing results of the MMS physical oceanography program to date, stated, with respect to ring movement, that:

> The general paths of Rings 1599, 3374, and 3350 are... identical. ... Three months elapsed from the time Ring 3350 was shed until it was seeded. Rings 1599 and 3374 indicate a three to five month travel time from seeding until encountering the Mexican coast. These results indicate a total travel time across the Gulf of Mexico of six to eight months.

Waddell (1986) further noted that drifter No. 3374 left its ring and moved eastward in a location (ca. 23.5 N), where large eastward transports of some 30 Sv had been observed by Merrell and Morrison (1981; Fig. 14). Eddies are translated to the north after encountering the western boundary, as explained by Smith and O'Brian (1983). Currents off the east coast of Mexico are probably dominated by eddies (Sturges, pers. comm.).

Waddell (1986) depicted the linear trajectories of nine separate rings that were followed for, "... a reasonably long and continuous period of time" (Fig. 9). Net movement of most of the rings was toward the southwest. Characteristic paths of warm rings based upon GOES and NOAA satellite data during the period 1973 to 1984, "...suggest that all paths converge to a region in the northwestern Gulf of Mexico best defined by 25 N to 28 N and 93 W to 96 W." Average ring diameters are estimated to be on the order of 185 km, and their westward translation speeds range from one to five km per day (Elliott, 1982). Including travel and spin-down time, the life span of an eddy shed by the Loop Current seems to be about nine months to a year.

Simulated drifter tracks generated from modeling experiments, and the actual path of drifter No. 1599 (Fig. 6) showed close agreement, and Wallcraft (1986) stated, "A persistent anticyclonic gyre in the northwest Gulf has been a feature of almost all Gulf simulations performed to date."

Shelf Currents

While significant progress has been made in understanding coupling between eastern and western Gulf circulation patterns, shelf-slope and basin surface current interactions are less clearly understood (Wang, 1983). Circulation of continental shelf waters of the eastern Gulf (Sturges and Evans, 1983; Sturges, 1986), will not be further discussed. Coastal and shelf circulation of the western Gulf is of principal interest here, since it is in these waters that Kemp's ridley hatchlings begin the pelagic phase of their life history.

As reviewed and discussed in Cochrane and Kelly (1985), wind is a primary cause of currents along much of the Texas-Louisiana coasts. The known effects of wind stress along other Gulf of Mexico coasts indicates that winds are probably of primary importance in directing surface water movements over and along the north-south trending coast of northeastern Mexico, as well (e.g., Sturges and

Blaha, 1976; Csanady, 1982; Brooks, 1984). Cochrane and Kelly (1985) quoted observations from an unpublished manuscript by D.L. Harrington entitled, "Oceanographic Observations on the Northwest Continental Shelf of the Gulf of Mexico 1963-1965", and cited other investigators whose conclusions were in agreement.

Based on drift bottle experiments, Herrington found that:

> (1) currents between September and April for the most part are alongshore westward along the Louisiana and southwestward along the Texas coast; (2) the reversal of the system usually starts around May or June when currents become irregular and obliquely offshore; (3) by July, currents are stronger northeasterly or easterly; this reversal usually prevails for a short time and by mid-August, the flow has returned to westward.

Cochrane and Kelly (1985) summarized their consideration of shelf circulation in the northwestern Gulf by stating that a cyclonic gyre prevails over much of the shelf except during July and August. Downcoast currents (west or south, with respect to shoreline orientation) dominate much of the coast except during July and August, and form the inner (i.e., shoreward) limb of the cyclone. A countercurrent (north, east, or northeastward flowing) is present near the shelf break, and includes the outer limb of the gyre. Part of the countercurrent extends south and east beyond the gyre. Water flows offshore in the gyre's southwestern limb, and toward the Louisiana coast in its eastern limb. In late August or September after an abrupt change in prevailing wind direction, which becomes again downcoast, the cyclonic gyre is reestablished and reaches its maximum southward extent beyond the Rio Grande. While the eastern limb of the gyre remains in place until July, the southwestern limb (in which surface water flows offshore) contracts to the east beginning in March or April due to increasingly southerly and southwesterly winds; by July, the gyre has disappeared. The overall picture of Texas-Louisiana shelf circulation dominated by a counterclockwise gyre is in agreement with the findings of Lewis (1984). The anticyclonic boundary current discussed above might possibly reinforce an eastward flowing surface current near the shelf break. Shaw et al. (1985) noted that juvenile organisms emigrating from estuaries along the Texas-Louisiana coasts during summer, would be carried eastward during the period of longshore current reversal discussed by Kelly et al. (1982) and Cochrane and Kelly (1986).

In the vicinity of Tamaulipas, Mexico, the continental shelf is much narrower than off the Louisiana-Texas coasts, and the slope is steeper (Fig. 10). Anticyclonic eddies in contact with the slope boundary are much closer to Kemp's ridley natal beaches at this latitude than further north, where the shelf broadens considerably.

Ocean Fronts and Convergence Zones

Surface water convergences of various types, and the role they play in concentrating buoyant objects and surface-associated (especially planktonic) organisms at sea may be a precondition for the survival of many species that live in the epipelagic zone according to Carr (1986b). The causes, types, and widespread occurrence of surface convergences were reviewed by Galt (1985). Detailed descriptions of certain observed ocean fronts and current convergences in the Gulf of Mexico were given by Wang (1983), Weisenberg (1983), and Shaw et al. (1985). Olson and Backus (1985) described some of the biological consequences of surface convergences, and Carr (1986) speculated on the importance of these concentrating mechanisms to the pelagic stages of sea turtles.

As noted, the surface circulation of the Gulf of Mexico is influenced by the Loop Current and its meanders and eddies. The outer edges of the Loop Current and its derivatives are thermal or density fronts which interact with coastal waters, river discharges, or the resident waters of the Gulf itself; downwelling may occur at these boundaries, although sloping density fronts *per se* may be regions of mixing rather than vertical water motion. Surface water convergence at a much smaller scale also occurs as a result of Langmuir circulation and other environmental conditions discussed by Butler et al. (1983) and Galt (1985). Direct evidence of ocean fronts can often be seen as abrupt changes in water color, temperature, salinity, sea surface roughness (Weisenberg, (1983), or in a rack line consisting of sargassum and floating debris that may extend, on occassion, for several miles (e.g., Carr, 1985; 1986). Less obvious indications of downwelling are sometimes evidenced offshore by exceptionally large catches of neuston at certain times (Collard, unpubl.), that were probably not attributable to patchiness (Cushing, 1962), or upwelling.

It is clear that surface convergences are widespread in the Gulf of Mexico; they are not stationary, however, but constantly change their positions as the currents and other conditions which lead to their formation vary over time.

PELAGIC STAGES OF KEMP'S RIDLEY AND MEAN GULF OF MEXICO CIRCULATION

Nearshore And Shelf Currents Off The Natal Beaches

Descriptions of sea conditions along the 17 km long primary nesting beach of Kemp's ridley, based upon visual observations (reviewed by Marques, 1986), indicate that it is an area of convergent onshore currents much of the time, and that onshore water movement is greater during storms (Hildebrand, 1963; Marquez, 1986). It was noted above that surface currents do not flow onshore, but alongshore except during certain heavy storms. A convergence of longshore currents off Tamaulipas has not been reported, and is unlikely. During the summer and early fall when Kemp's ridley hatchlings enter the water, they often, or usually encounter surf into which they swim toward the open sea. It is presumed that

Kemp's ridleys spend a year or more in the open sea, and a successful swim frenzy period would place the young turtles in the vicinity of a boundary current which might transport them there.

With the possible exception of a strong southerly longshore flow, the direction of local nearshore currents is probably of less significance to the turtles' initial heading than other orientation cues such as horizon brightness. Hatchling sea turtles have been observed to make compensatory course changes to currents which would vector them back toward the beach (see Part 1). In conditions of heavy waves, hatchlings might be thrown back upon the beach, where they would likely perish.

If it is assumed that Kemp's ridley neonates swim vigorously for 24 hours or so upon entering the water for the first time; that they swim in a direction normal to the beach; and can maintain, in the absence of strong adverse currents, an average speed of about one knot or so (perhaps an overly optimistic estimate), the turtles would have to swim for about a day before they encountered the Mexican Current at the shelf/slope boundary. This amount of effort in terms of energy reserves (yolk) seems to be within the capabilities of Kemp's ridley neonates. In the simplest case, assuming that vigorous swimming stereotypically lasts for a fixed period of time (unknown for Kemp's ridley), the hatchlings should reach the shelf break, and encounter a western boundary current near the end of the swim frenzy period. The swim frenzy may last for longer than 24 hours, in which case further swimming would more deeply embed them in the current, to their potential advantage.

In the presence of adverse currents (i.e., those currents inhibiting seaward movement), hatchlings may be able to extend the duration of the swim frenzy period until they encounter a boundary current (a form of purposeful search behavior for which there is no evidence), or swim more slowly until a favorable current is encountered*, or simply drift.

Transport of Hatchlings In The Western Gulf of Mexico

All anticyclonic eddies derived from the Loop Current translate to the west or southwest across the western basin of the Gulf of Mexico, and contact the shelf/slope boundary of Texas or Mexico. As they begin to contact the slope these eddies subsequently move to the north either independently or after coalescing with another eddy in the same area. Exactly what happens is not well known. These anticyclonic eddies together result in a boundary current which seems to flow to the north for most of the time in any given year, during a majority of years for which records are available. This flow will continue to the north until it reaches an area dominated by a cyclonic eddy (see Merrill and Morrison, 1981; Fig. 14). As it approaches the northwestern corner of the Gulf, the flow is in an easterly direction. As discussed earlier, the area between the southern limb of a cyclonic eddy, and the northern limb

of an anticyclone often results in an eastward jet of some magnitude flowing between them. When found in satellite pictures, the offshore easterly jets are quite striking.

A number of distributional scenarios may be postulated for Kemp's ridley hatchlings once they have crossed the continental shelf off Mexico. First, they may be captured within an anticyclonic eddy that remains in the western Gulf (Fig. 8), and thus spend the entire pelagic phase there. Second, hatchlings may be swept to the east off the Texas-Louisiana shelf, to be entrained in the Loop Current. Depending upon transit time from the western to the eastern Gulf, and whether the hatchlings fetch up in a northeastern Gulf eddy, and are carried back into the western basin or fetch up in the northern Loop and leave the pelagic zone for the Panhandle of Florida, some of the young turtles are carried out of the Gulf of Mexico through the Straits of Florida, and drift with and along the western edge of the Florida Current/Gulf Stream until they are old enough and/or strong enough to leave the current and disperse shoreward. Individuals that do not exit the Gulf Stream system by swimming or being blown to the west by winds are probably lost to the population.

While the net movement of the pelagic stage of Kemp's ridley is probably chiefly attributable to surface watermass movement, the hatchlings may be capable of substantive position changes within currents. It is entirely possible that some of the hatchlings escape from a given current, to be swept into another one; perhaps into one with an entirely different future path or lifespan. In fact, it may be misleading to describe the hatchlings' life style as planktonic until they assume a shallow water demersal existence as juveniles. Hatchling sea turtles are capable of swimming speeds greater than those of most zooplankters, and they possibly "search for" concentrations of sargassum or other floating objects under or within which they may obtain food or shelter. "Searching" may involve no more (nor does it need to) than swimming downstream or across current in the absence of aggregations of floating objects. The same mechanisms that cause sargassum to converge would bring in small turtles, and except to counter wind drift, no swimming at all may be required by the turtles to "find" sargassum.

Overview Of Currents And The Dispersion of Pelagic Kemp's Ridley

The narrow shelf off Rancho Nuevo may enhance the probability of neonates reaching a western boundary current or an anticyclonic eddy. Once entrained in a current, neonate turtles are probably, but not certainly, committed to completing the pelagic, dispersal phase of their lives in the same direction, and at the same speed as the host current path dictates. Although available information is clearly inadequate to make unequivocal predictions, four distributional patterns for neonate/hatchling Kemp's ridleys seem more likely to me than than the many others that can be suggested. 1.) They remain in the central-southwestern Gulf of Mexico. 2.) They are swept out of the western Gulf, are entrained by the Loop Current, and finish the pelagic phase in the Florida Current/Gulf

Stream. 3.) As in (2.), but they are captured by a northern Loop Current eddy, and return to the western Gulf. 4.) They do not make it to a major dispersing current, or are ejected from a current (as Langrangian drifters may be); find themselves in coastal waters, and perish there because of presumably higher predation pressure or cold winter temperatures not found in the Loop or Florida Currents. 5.) As an alternative to (4.), older individuals of post-pelagic size (ca. 20 cm) might find themselves in coastal waters, their subsequent developmental habitat, and survive there as benthic carnivores.

Unanswered Questions

It is difficult to find drifting objects at sea unless they are conspicuous because of their size, color, radio signatures or (as Sturges, pers. comm., suggested), their "food" signatures. If hatchling Kemp's ridleys swim within a moving watermass, they will be difficult or impossible to locate a short time after they leave the beach. If they are relatively passive drifters; or they actively seek out, or fetch up in sargassum drift lines; or, if their innate behavior is such that they are obligatory associates of sargassum when it can be found by them, it may be possible to find them at sea with the use of real-time satellite imagery, aircraft-aided location of driftlines, dedicated ship time, and an in-the-water approach by swimmers.

The present discussion has not addressed some important questions. Among them: what if any, internal or environmental cues induce post-hatchling turtles to quit the pelagic environment; what proportion of a given year class are lost because of unfavorable dispersion by currents and/or winds; what role, if any, does sargassum play in the survival of the pelagic stage; how do preadults and returning adults make their way back to Rancho Nuevo to breed; does the swim frenzy period last for a predetermined period of time; what and how often must the turtles eat; do Kemp's ridley hatchlings exhibit goal-seeking behavior to find or recognize currents or sargassum. Additional questions include the extent and frequency of swimming by the turtles that may occur within or between currents and watermasses, and the relative importance of winds and wave transport in their dispersion. The most obvious and least discussed problem has to do with the fact that Kemp's ridley hatchlings do not encounter mean circulation patterns when they leave the natal beach. Each cohort of neonate turtles is exposed to real-time oceanographic conditions, and at present we do not know what those are.

SUMMARY AND CONCLUSIONS

Enough is known about mean circulation patterns in the Gulf of Mexico and distributional end points of Kemp's ridley to suggest slightly more detailed distributional hypotheses for the pelagic phase than historically possible. Actual dispersal patterns are not known.

On average, circulation in the western Gulf is dominated by rings from the Loop Current. Some anticyclonic eddies derived from the Loop Current drift in a westerly direction and become boundary currents in the western Gulf. Consideration is given to how neonate Kemp's ridleys cross the continental shelf off Rancho Nuevo, and are entrained in these boundary currents, or in anticyclonic eddies. Pelagic hatchlings either remain in the western Gulf, or are transported to the Florida Current via coupling of an eastward flowing jet in the northwestern Gulf with the Loop Current, which exits through the Straits of Florida. Several permutations of these two basic patterns are discussed.

Consideration of the frequency and position of surface convergences relative to the likely positions of hatchlings indicates that the turtles probably encounter drift lines or accumulations of floating objects rather frequently. The important questions of how often they do, or whether an association with sargassum is of adaptive advantage are not known.

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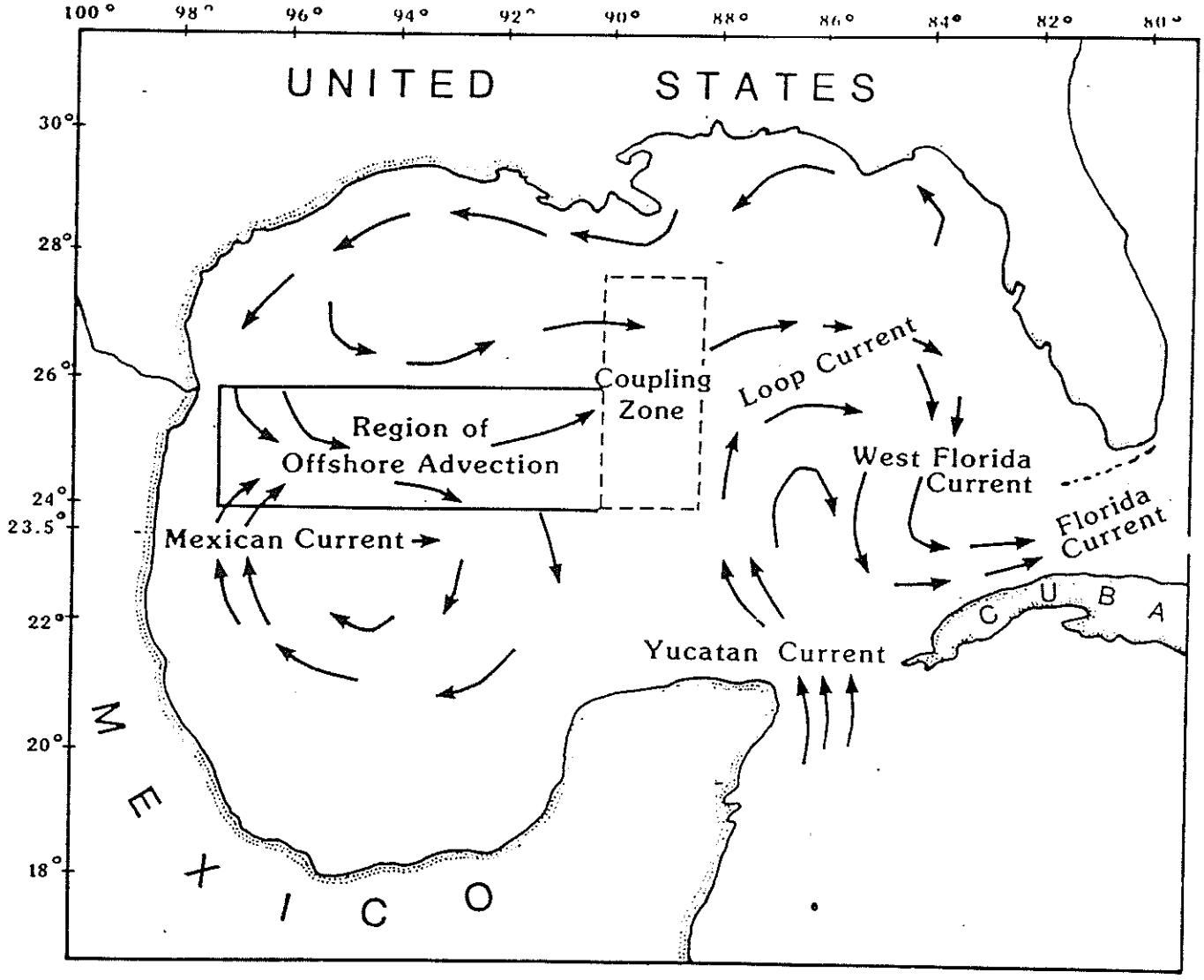
1 Bruchs' suggested generalized circulation regime in the Gulf of Mexico showing the region of coupling between the eastern and western basins. (Redrawn from Bruchs, pers. comm.).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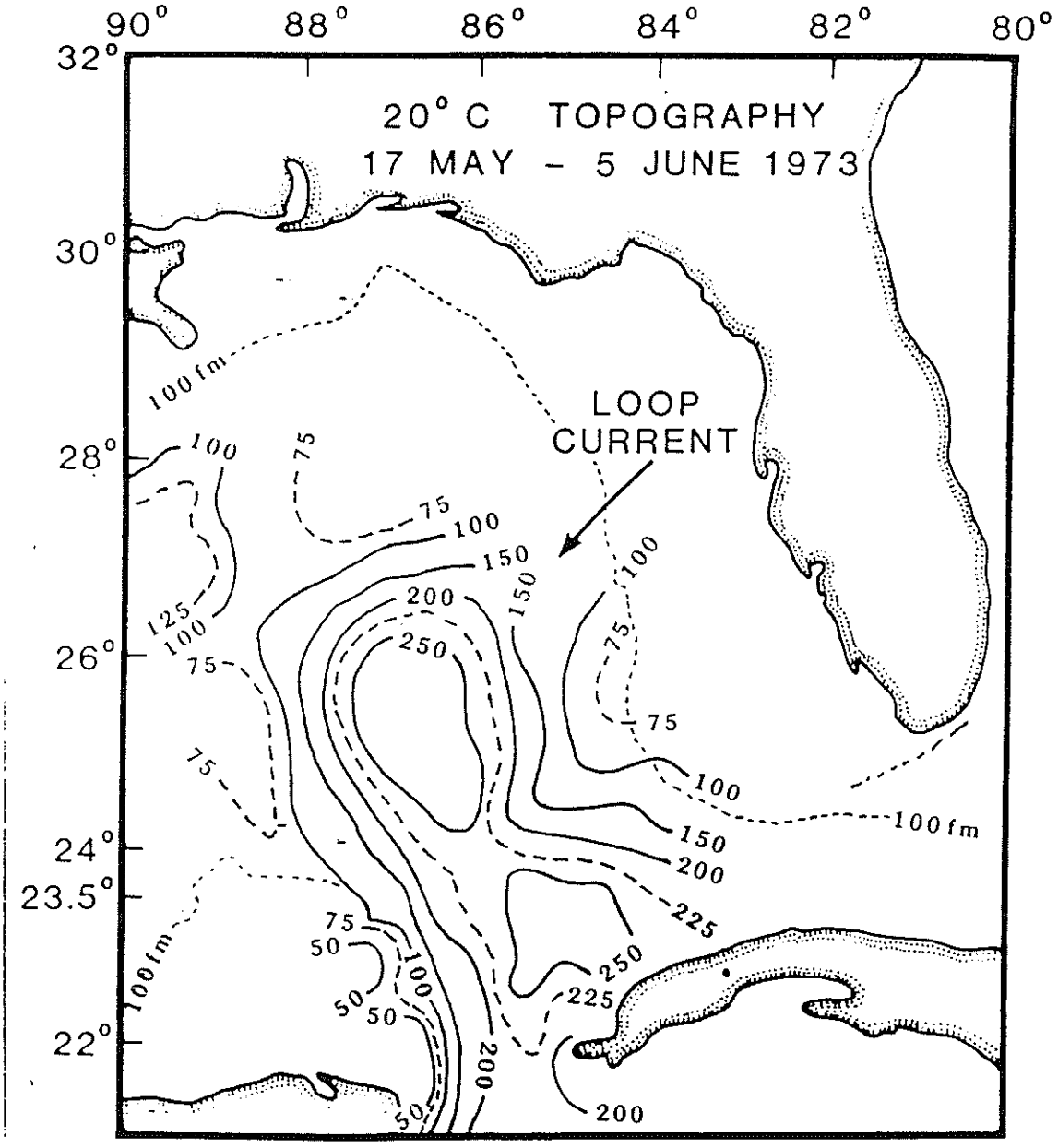
Coupling Zone
Region of Offshore Advection
Loop Current
West Florida Current
Florida Current
Mexican Current
Yucatan Current
CUBA
MEXICO

2 Depth of the 20 C isotherm during May and June 1973, showing the position of the Loop Current intrusion. (Adapted from Molinari et al., 1977, fig. 1A).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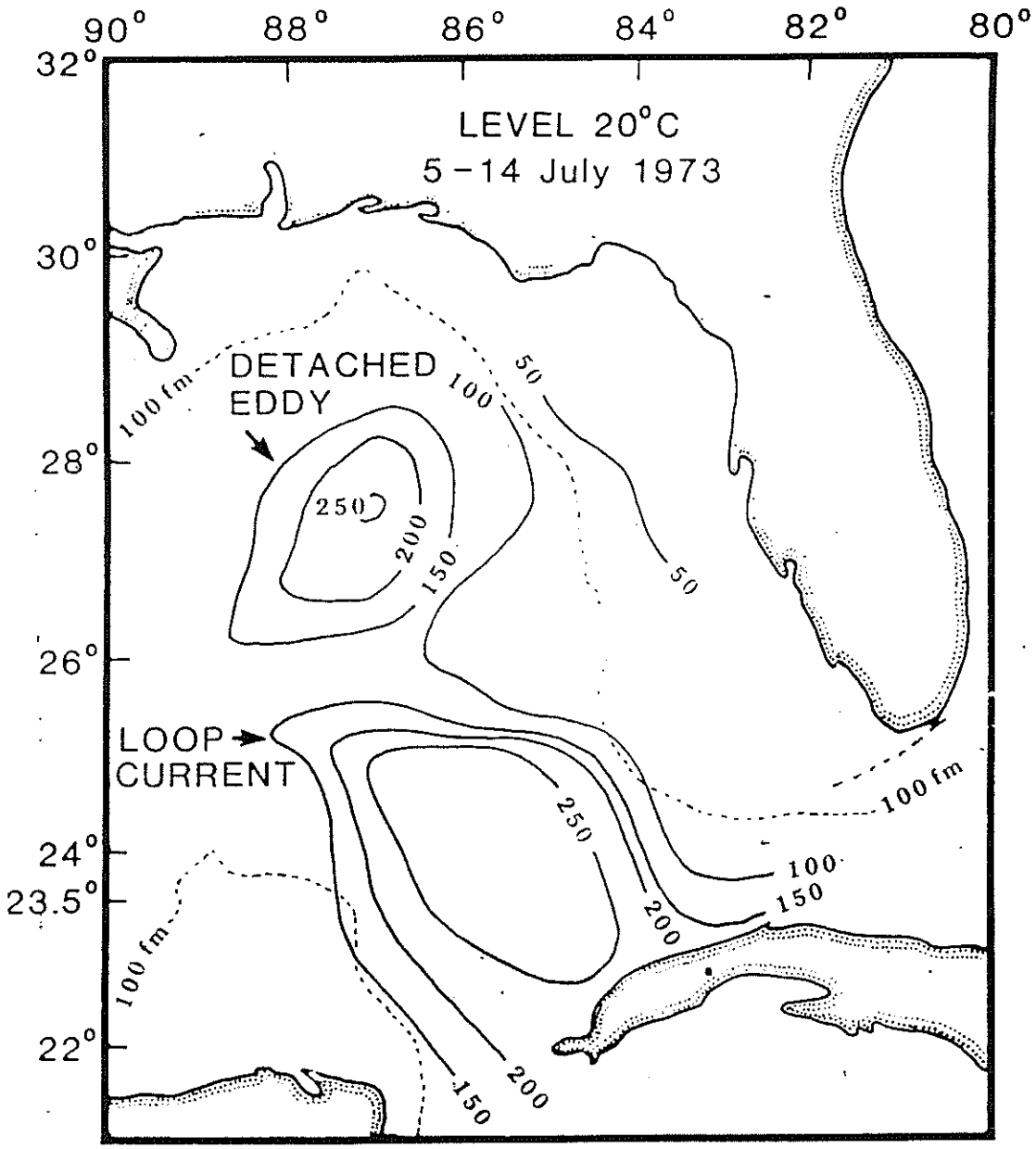
20° C TOPOGRAPHY
17 MAY - 5 JUNE 1973
LOOP
CURRENT
100 fm
100
75
125
150
200
250
225
50
100 fm

3 Depth of the 20 C isotherm during July 1973, after a Loop Current eddy has been pinched off. (Adapted from Molinari et al., 1977, fig. 1B).



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LEVEL 20°C
5-14 July 1973
DETACHED
EDDY
LOOP
CURRENT
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50
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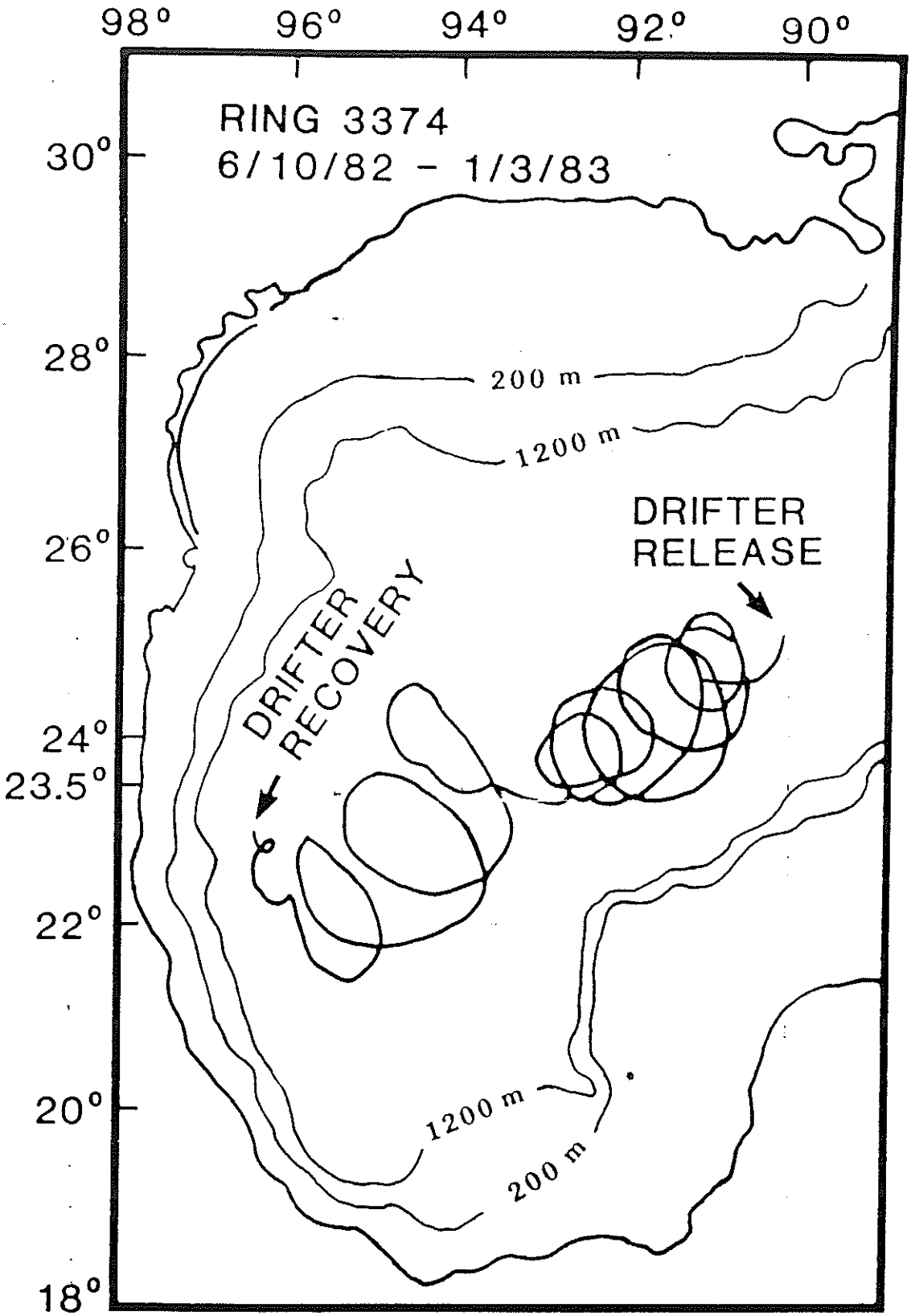
4 Trajectory of Lagrangian drifter number 3374 tracked from 6 October 1982 to 1 March 1983. (Adapted from Lewis, 1984, fig. 4.2-50B).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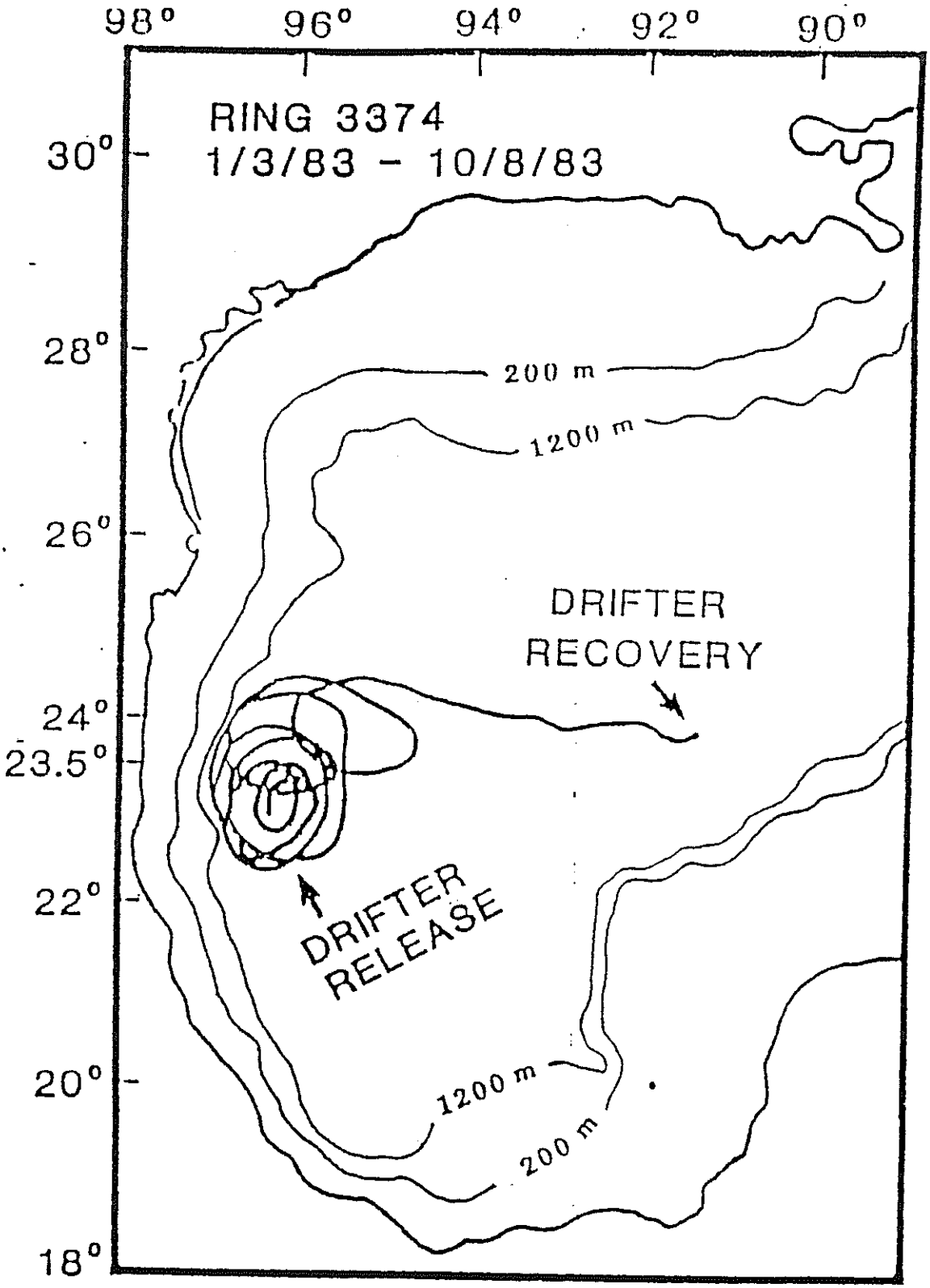
RING 3374
6/10/82 - 1/3/83
200 m
1200 m
DRIFTER
RELEASE
DRIFTER
RECOVERY
1200 m
200 m

5 Trajectory of Lagrangian drifter number 3374 tracked from 1 March 1983 to 10 August 1983. (Adapted from Lewis, 1984, fig. 4.2-50C).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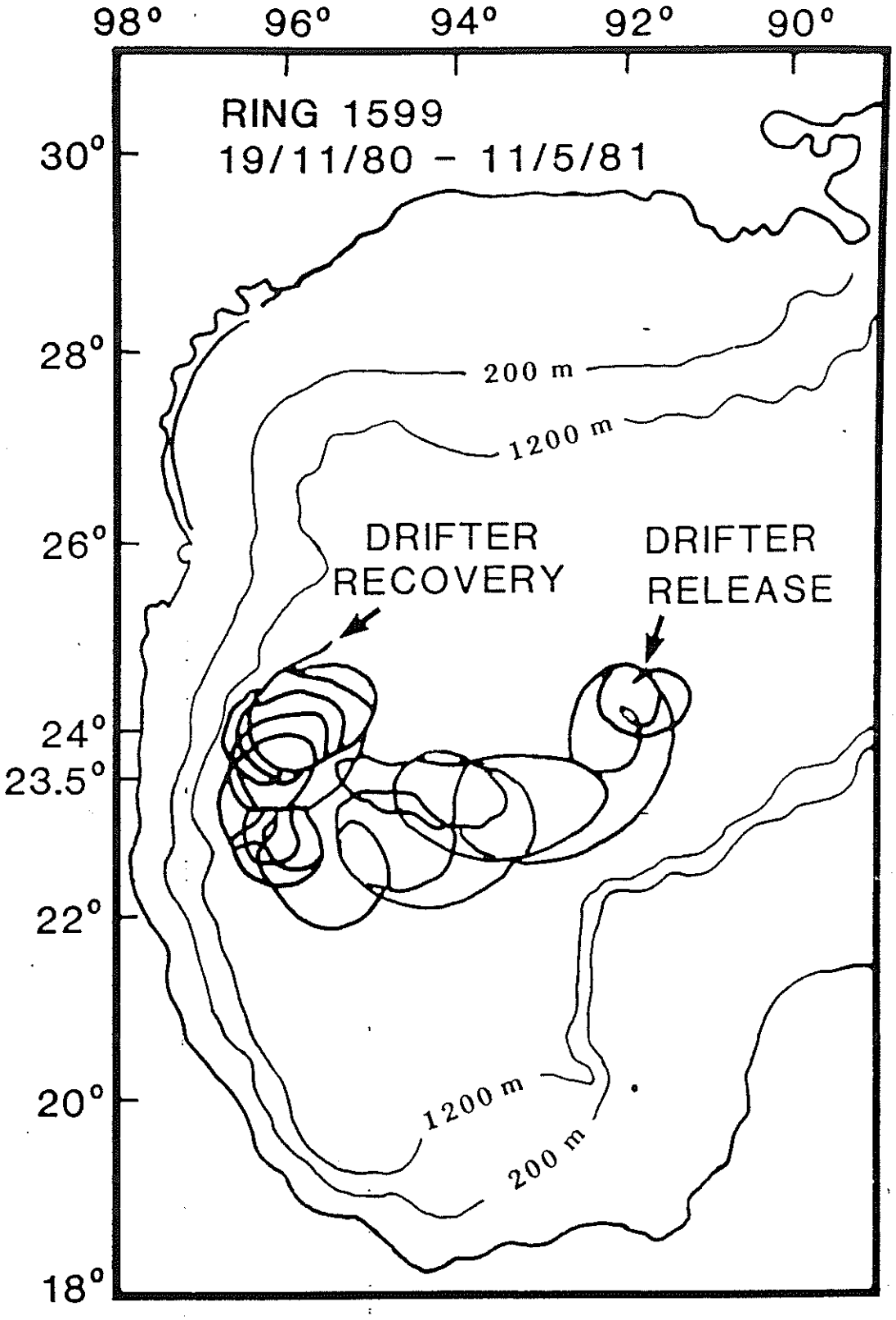
RING 3374
1/3/83 - 10/8/83
200 m
1200 m
DRIFTER
RECOVERY
DRIFTER
RELEASE
1200 m
200 m

6 Trajectory of Lagrangian drifter number 1599 tracked from 19 November 1980 to 11 May 1981. (Adapted from Lewis, 1986, fig. 3C-6).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90°
RING 1599
19/11/80 - 11/5/81
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28°
26°
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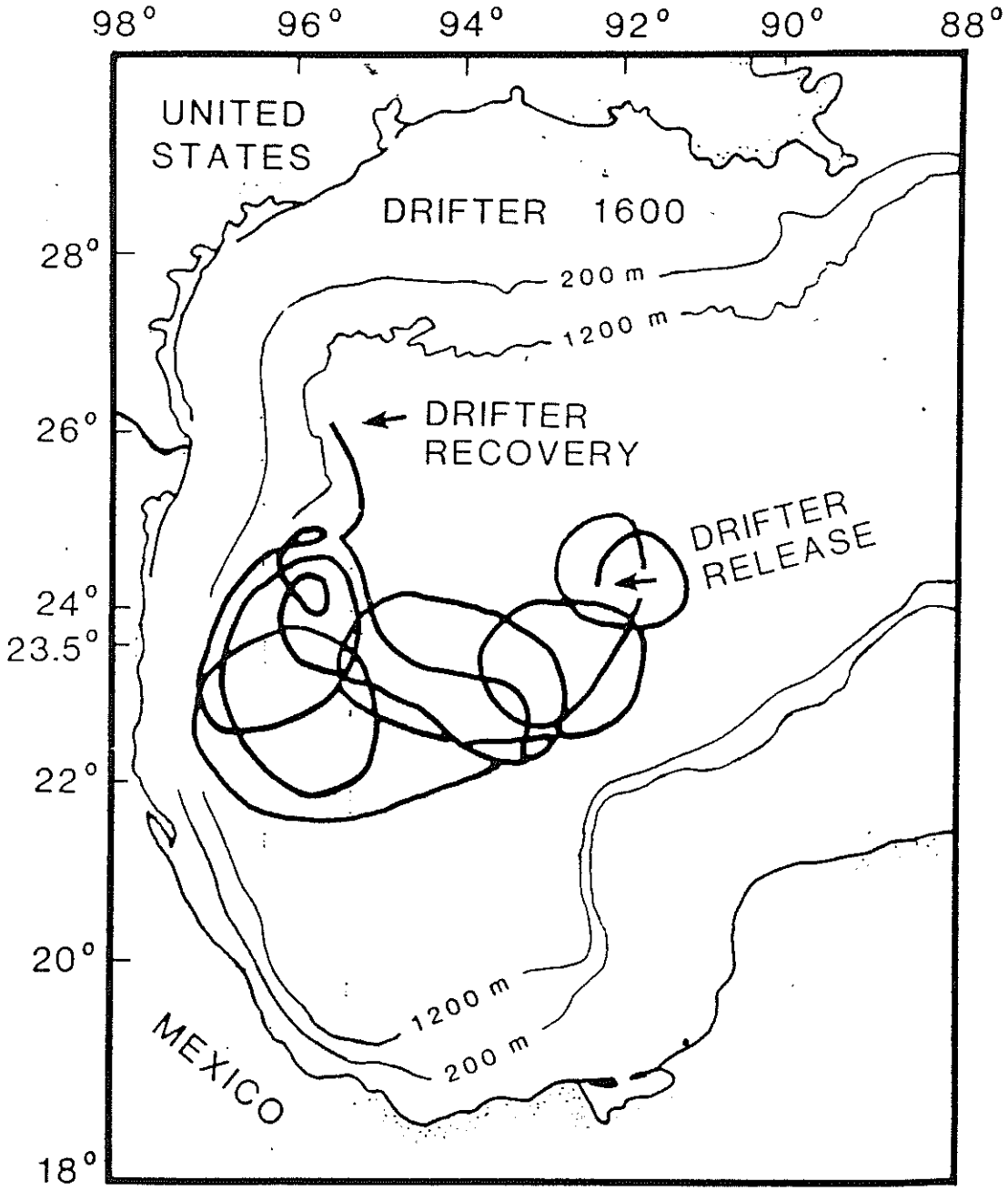
23.5°
22°
20°
18°
200 m
1200 m
DRIFTER
RECOVERY
DRIFTER
RELEASE
1200 m
200 m

7 Trajectory of Lagrangian drifter number 1600 tracked from 20 November 1980 to 11 May 1981. (Adapted from Kirwan et al., 1984, fig. 1C).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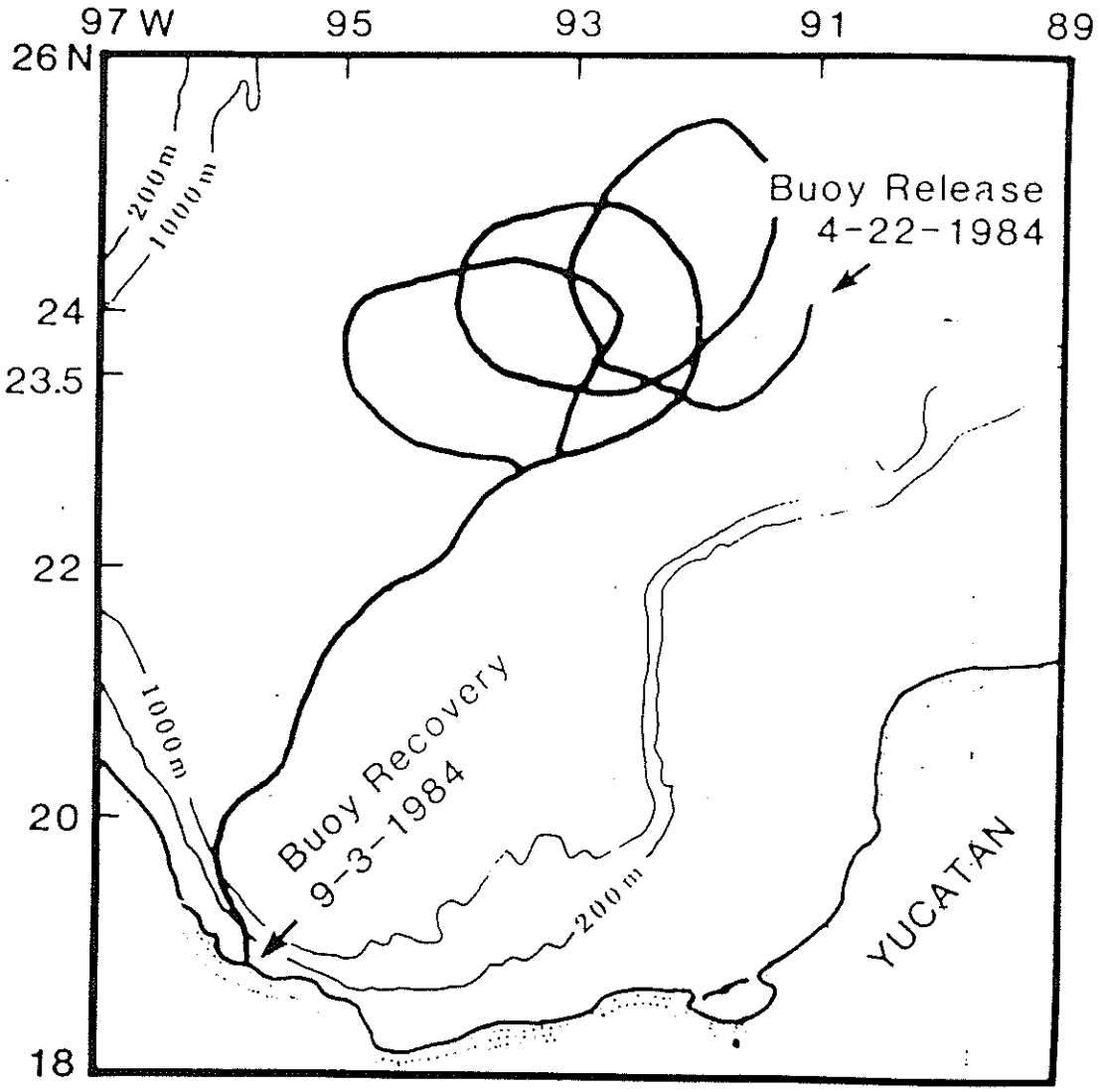
UNITED
STATES
DRIFTER 1600
28°
200 m
1200 m
26°
DRIFTER
RECOVERY
DRIFTER
RELEASE
24°
23.5°
22°
20°
1200 m
200 m
MEXICO
18°

8 Trajectory of Lagrangian drifter number 3350 tracked from 22 April 1984 to 3 September 1984. (Adapted from Waddell, 1984, fig. 41).


97 W
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89
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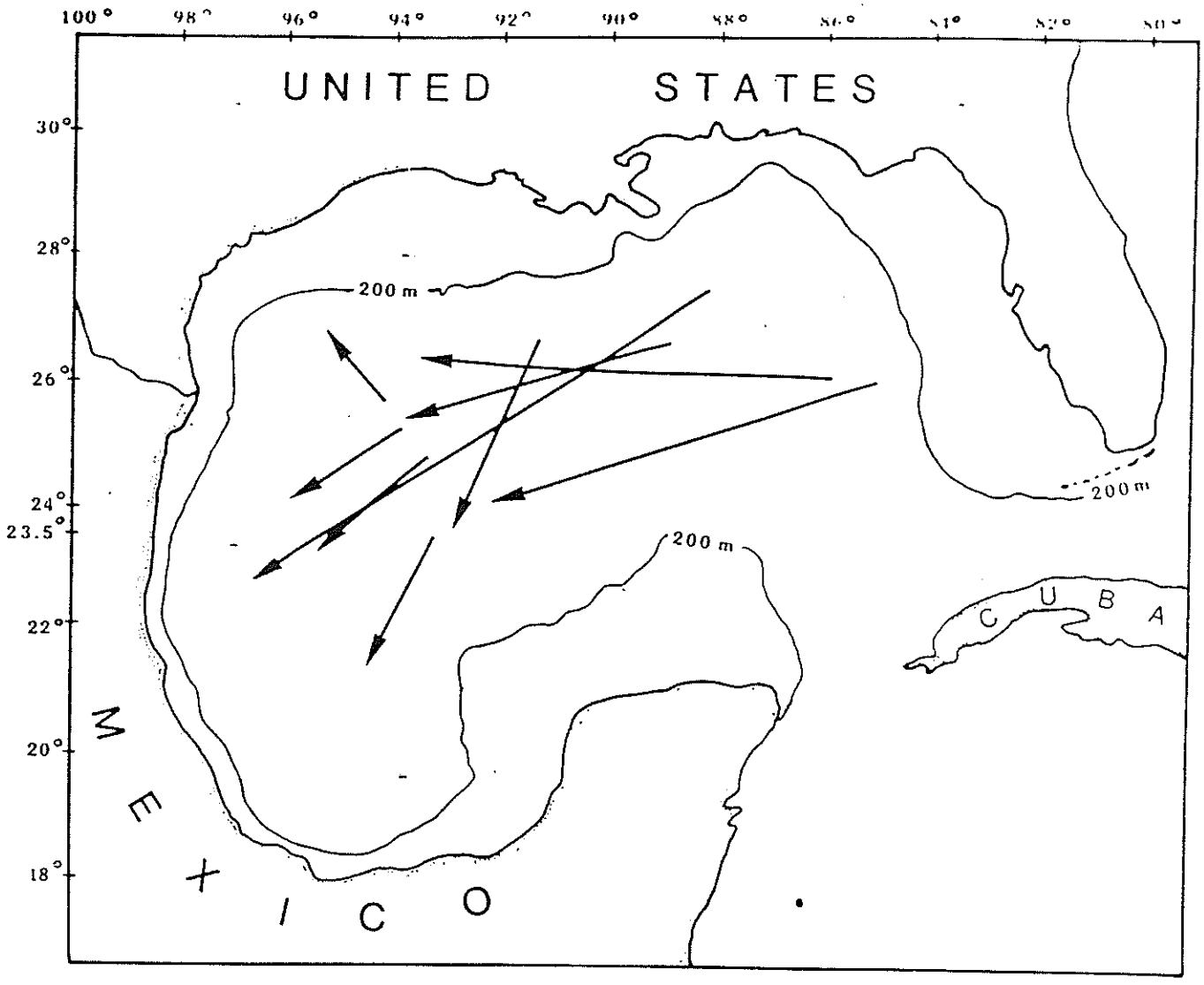
23.5
22
20
18
200m
1000m
Buoy Release
4-22-1984
1000m
Buoy Recovery
9-3-1984
200m
YUCATAN

9 Linear paths based on the connection of endpoints of nine different Loop Current rings as evidenced by the movements of Lagrangian drifter buoys. (After Waddell, 1986, fig. 4.3-35).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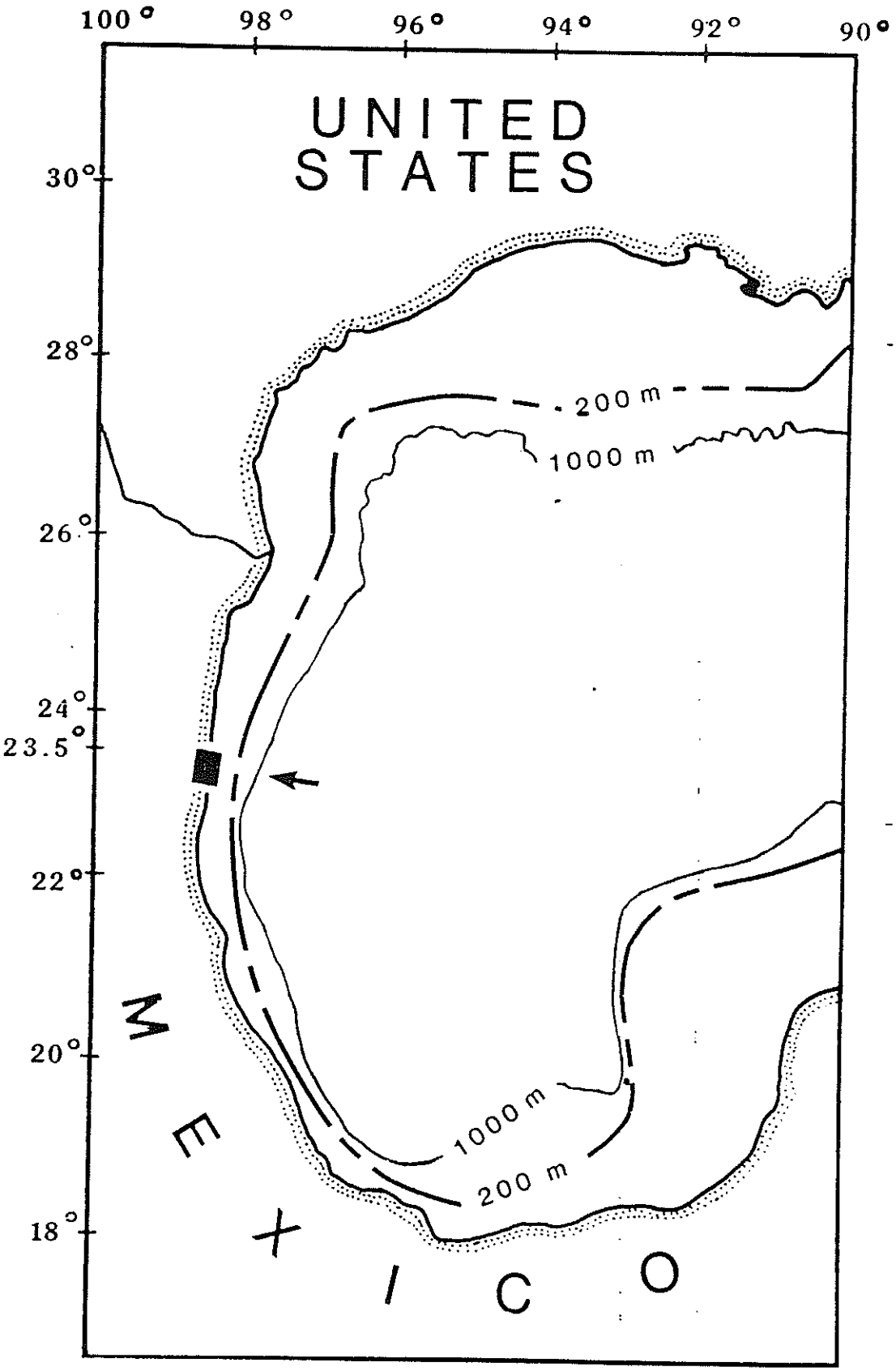
200 m
200 m
200 m
MEXICO
CUBA

10 Proximity of the shelf break (200 m) off Rancho Nuevo, Mexico (23 11' N). (Adapted from U.S. Dept. Commerce, 1985; fig. 1.01).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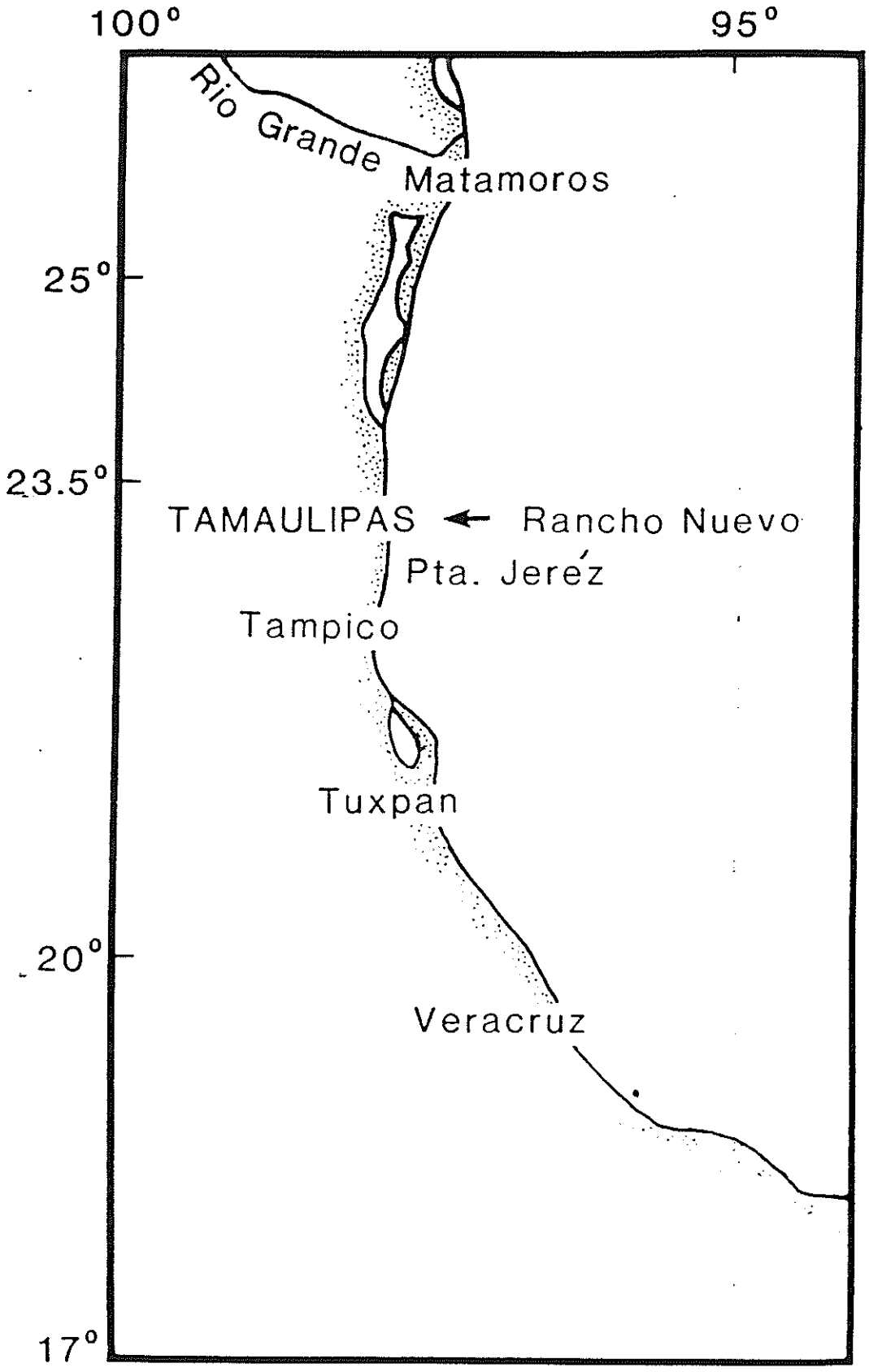
11 Location of Rancho Nuevo. (Adapted from Marquez, 1978; fig. 1).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Rancho Nuevo
Pta. Jereźz
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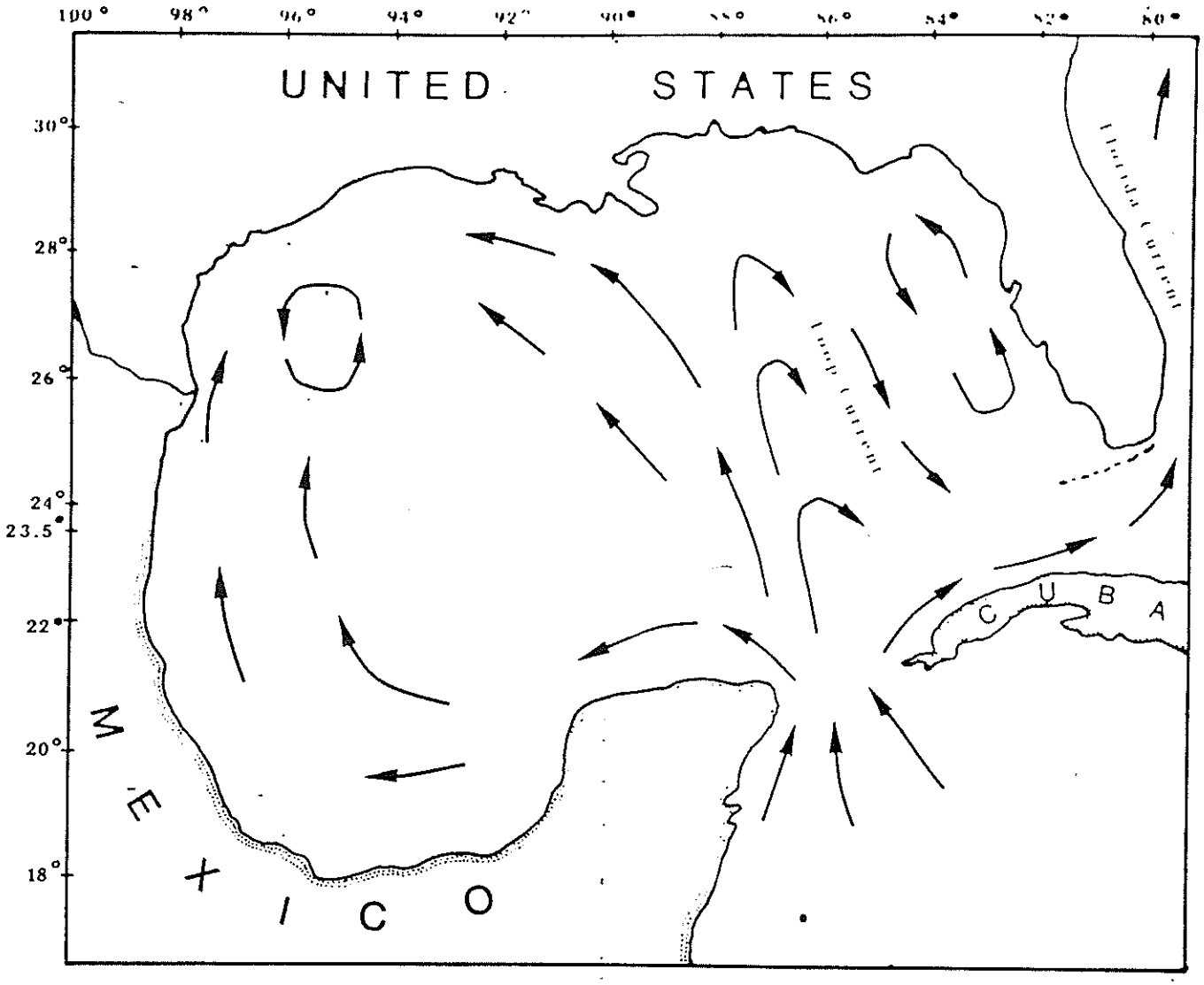
Veracruz
17°

12 Generalized surface currents in the Gulf of Mexico. (Adapted from Galloway, 1981).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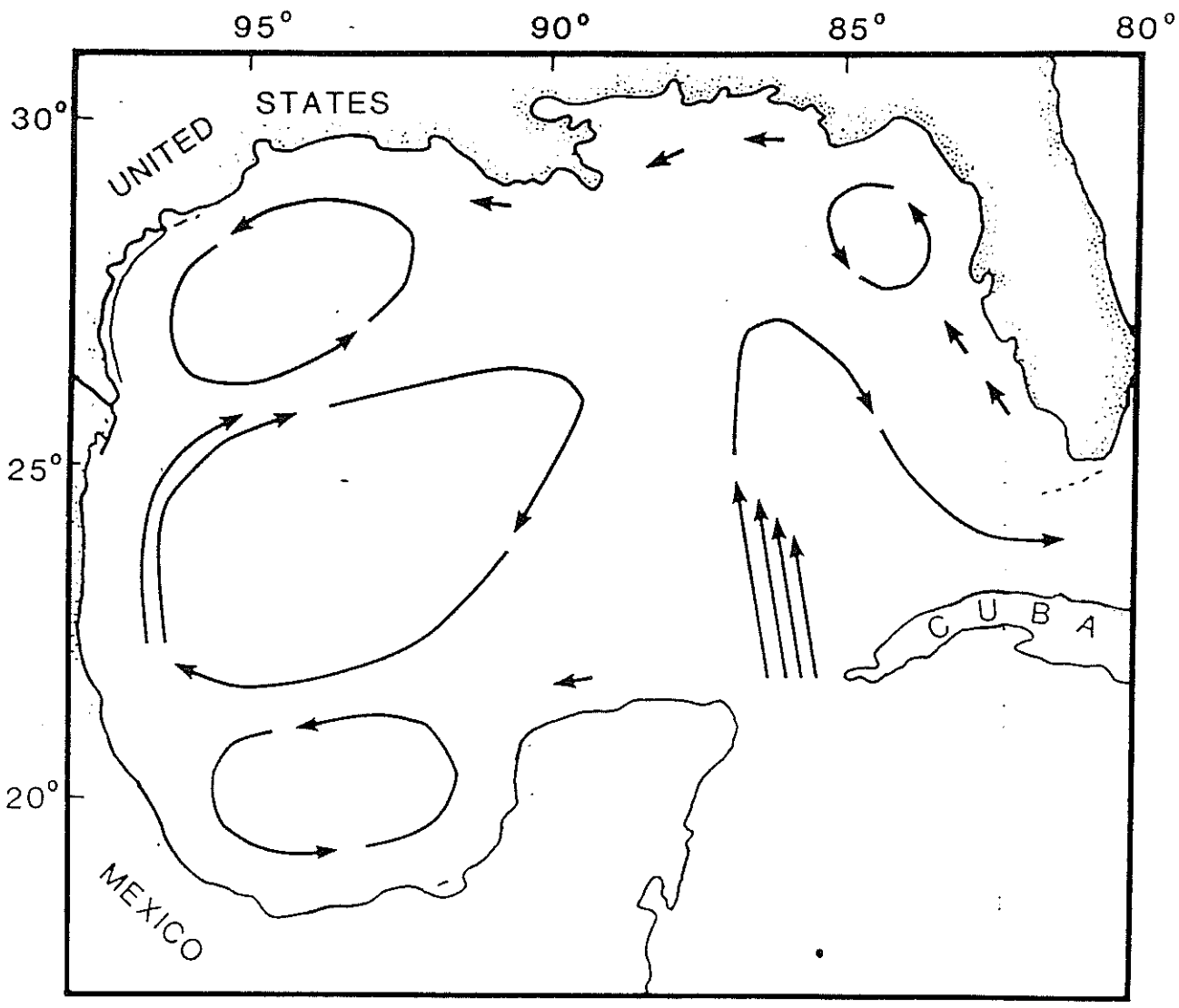
Florida Current
Loop Current
CUBA
MEXICO

13 Mean circulation of the Gulf of Mexico as suggested by Sturges et al. (From Sturges' Fig. 1, in Sturges and Shang, 1978).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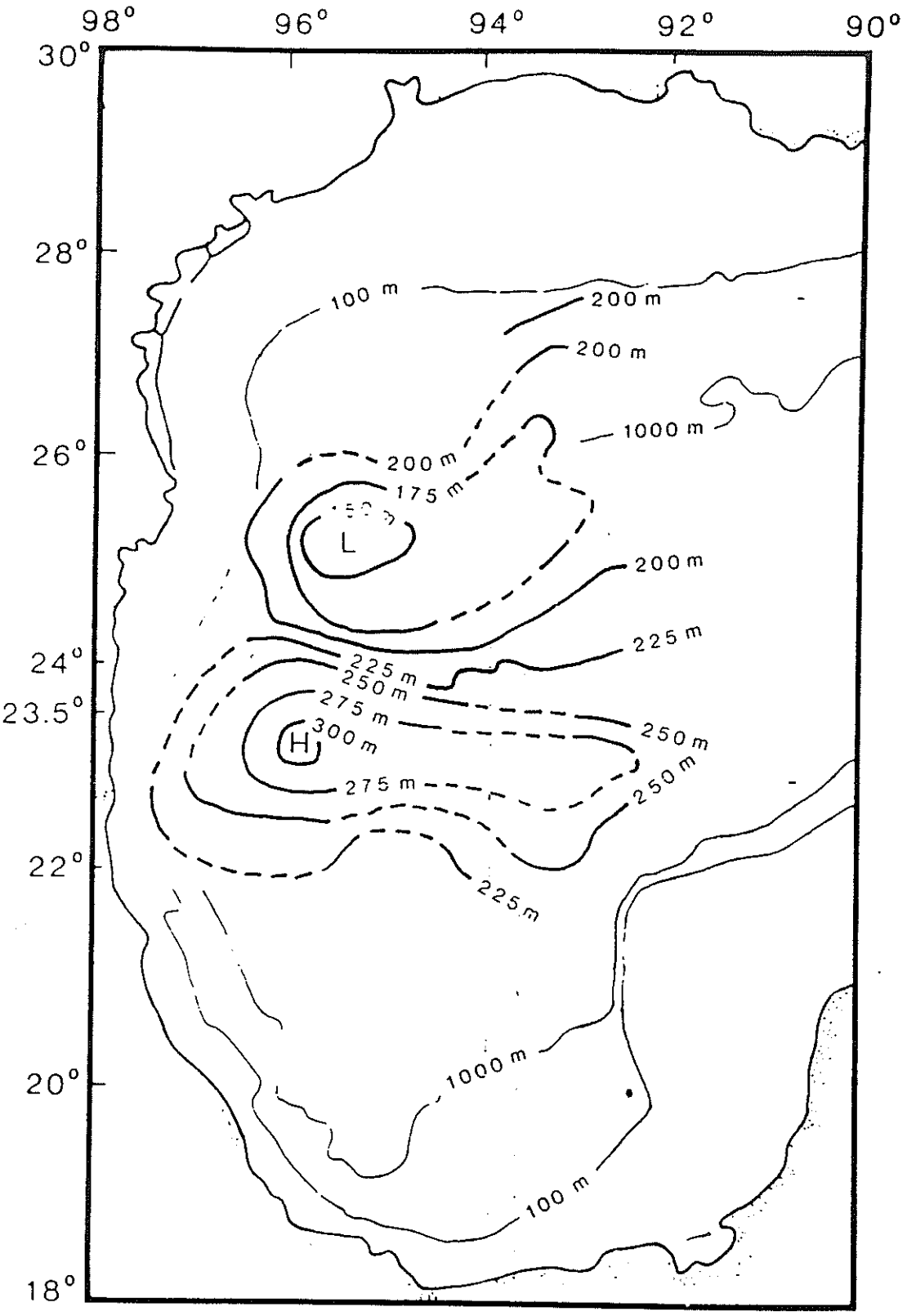
UNITED STATES
MEXICO
CUBA

14 Counter-rotating vortices in the western Gulf of Mexico near Rancho Nuevo. Water flows to the east between the northern cyclone and the southern anticyclone. (Adapted from Merrill and Morrison, 1981).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